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Abstract

Indirect sexual selection arises when reproductive individuals choose their mates based on heritable ornaments that are genetically correlated to fitness. Evidence for genetic associations between ornamental coloration and fitness remain scarce. In this study we investigate the quantitative genetic relationship between different aspects of tail structural coloration (brightness, hue and UV chroma) and performance (cell mediated immunity, body mass and wing length) in blue tit (*Cyanistes caeruleus*) nestlings. In line with previous studies, we find low heritability for structural coloration and moderate heritability for performance measures. Multivariate animal models show positive genetic correlations between the three measures of performance, indicating quantitative genetic variation for overall performance while tail brightness and UV chroma, two genetically independent color measures, are genetically correlated with performance (positively and negatively respectively). Our results suggest that mate choice based on independent aspects of tail coloration can have fitness payoffs in blue tits and provide support for the indirect benefits hypothesis. However, low heritability of tail structural coloration implies that indirect sexual selection on mate choice for this ornament will be a weak evolutionary force.

Keywords: Sexual selection, coloration, good genes, genetic correlation, G matrix, heritability, *Cyanistes caeruleus*, wild, immune response

Introduction

Sexual selection theory has provided a powerful framework to understand the existence and function of ornaments. Reproductive individuals are predicted to choose their mates based on potential direct benefits (“good parent”) or indirect benefits (“good genes”) that they provide (Kirkpatrick & Barton 1997). In particular, the good genes model implies that genes increasing fitness can be phenotypically signaled by individuals, for example through ornamentation. While direct benefits models of mate choice have been well supported empirically, the indirect benefits models requires that ornaments and fitness are heritable and positively genetically correlated (Kirkpatrick & Barton 1997), which thus far is lacking evidence (Jones & Ratterman 2009).

Birds often exhibit colorful plumage patches, which have been extensively studied in relation to mate choice and intra-sexual competition (Amundsen 2000). In particular, box-breeding birds are ideal study systems to test for indirect benefits of ornaments because they allow long-term monitoring and cross-fostering experiment. Indeed, the combination of pedigree data obtained through long-term monitoring, and cross-fostering can be effectively used to decompose environmental from genetic resemblance between relatives (Kruuk & Hadfield 2007). Cross-fostering experiments are used to separately estimate the effects of foster and genetic parents’ traits on offspring performance (e.g. growth, mass, immunity) or viability, the former capturing direct effects (through parental care) and the latter capturing indirect (genetic) effects (assuming the absence of early environmental and maternal effects). In great tits (*Parus major*) for example, such experiments have provided support for direct and indirect benefits of carotenoid and melanin-based coloration in males and females. Indeed, great tits with a larger black breast stripe were found to produce more viable or heavier young (Norris 1993, Remeš & Matysiokova 2013) while yellower males and females with a blacker breast stripe were found to raise heavier nestlings (Pickett et al. 2013).

In combination with cross-fostering, quantitative genetics, which use information on the relatedness between individuals derived from the population pedigree, are particularly relevant to study sexual selection (Reid 2014). Indeed, this approach allows disentangling early environmental or maternal effects from additive genetic effects causing resemblance between relatives (Kruuk & Hadfield 2007), which cannot be done using only cross-fostering. In practice, a (co)variance partitioning approach implemented using (multivariate) mixed models, can be used to estimate the heritability of ornaments, fitness and their genetic correlation along with other sources of variance in and covariance between them (e.g. year, mother, nest of rearing). Earlier quantitative genetic studies find low heritability for structural and carotenoid-based ornaments (Hadfield et al. 2006, Evans & Sheldon 2012, Drobniak et al. 2013, Charmantier et al. 2017), as well as recruitment (Hadfield et al. 2006) in blue tits (*Cyanistes caeruleus*). In contrast, performance traits which are correlates of fitness, such as body condition or growth in nestlings, are found to be moderately heritable in collared flycatchers (*Ficedula albicollis*, Merilä et al. 2001, Pitala et al. 2007) and blue tits (Hadfield et al. 2007). To our knowledge, only two studies estimated the genetic correlation between a structural color ornament and fitness, and did not find support for the indirect benefits hypothesis (Hadfield et al. 2006, Qvarnström et al. 2006).

Under a particular case of the indirect benefits hypothesis, the “parasite-mediated sexual selection” (PMSS) hypothesis (cf. Hamilton & Zuk 1982), individuals’ sexual ornaments are predicted to signal immunocompetence. This hypothesis is based on the idea that cycles of coadaptation between hosts and parasites, which maintain additive genetic variation in resistance and thus fitness in hosts, can promote sexual selection for displays that signal resistance. Within species exposed to various chronic parasites, showiness is hence predicted to signal resistance to a wide variety of parasites. One common proxy of immunocompetence is the T-cell mediated immune response, assayed using phytohaemagglutinin (PHA). Although

PHA was shown to be condition-dependent (Alonso-Alvarez & Tella 2001, Thompson et al. 2014), several studies showed that it is heritable in various bird populations and species (Pitala et al. 2007, Bonneaud et al. 2009, Kinnard & Westneat 2009, Kim et al. 2013, Sakaluk et al. 2014). To date, the few cross-fostering studies testing the association between males' or females' ornaments and nestlings' PHA find mixed evidence for the presence of such relationship. In the blue-footed booby (*Sula nebouxii*), Velando et al. (2005) found no correlation between nestling PHA and father's foot coloration while in great tits, Pickett et al. (2013) found a positive correlation between nestlings' PHA and genetic father's but not mother's yellow plumage brightness. In the same species, Remeš & Matysiokova (2013) found that females with more immaculate white cheeks produce offspring with a higher PHA. In addition, only two studies estimated genetic correlations between coloration and PHA in adult male zebra finches (*Taeniopygia guttata*, Birkhead et al. 2006) and in common kestrel nestlings (*Falco tinnunculus*, Kim et al. 2013) and did not support the PMSS hypothesis.

Therefore, empirical evidence for the indirect fitness benefits and PMSS hypotheses remains equivocal, and more quantitative genetic studies are needed to gain insights into the evolution of color ornaments through sexual selection. In the present study, we investigate the quantitative genetic association between blue ornamentation and performance in blue tit nestlings. In this species, structural colors, in particular the blue cap of adults, have been extensively studied. This ornament has been shown to be sexually dimorphic (Hunt et al. 1998) and involved in mate choice (Andersson et al. 1998, Hunt et al. 1999) and intra-sexual competition (Alonso-Alvarez et al. 2004, Remy et al. 2010). In addition to their cap, blue tits show sexually dimorphic blue coloration of their tail feathers, which is already detectable at the nestling stage (Johnsen et al. 2003). Because most birds do not molt their tail feathers during their first year (Peters et al. 2007, Svensson 1992), the structural coloration of tail feathers may be involved in sexual selection. Here, we estimate genetic correlations between different aspects of tail

structural color (brightness, hue, UV chroma) and different performance measures (PHA, body mass, and wing length) using a multivariate animal model. This study provides rare estimates of genetic correlations between color and performance and supports the indirect benefits hypothesis.

Material & Methods

Measures of blue tit nestlings

Blue tits were studied in a nest-box breeding population in south-west Finland (Tammisaari, 60°01' N, 23°31' E). Hatch date of a brood (day 0) was established by daily checks. When the offspring were 2 days old (2005-2009), approximately half of each brood (on average 42±9%) was reciprocally swapped between a pair of nests with same aged and similar sized offspring (average brood mass at day 0). Nestlings were weighed and individually marked by clipping their nails. Whether the heaviest nestling was cross-fostered or not was decided at random and this action was subsequently alternated down the mass ranking of offspring (for more details see Brommer & Kluen 2012). When nestlings were 13 days old, the thickness of their wing web after feather removal was measured (to the nearest 0.01mm) two times using a spessimetre (Mitutoya 700-117SU, modified by the removal of a spring). Nestlings were injected with 0.04 ml of a solution of 5mg ml⁻¹ Phytohaemagglutinin (Sigma code L-8754) in saline. After 24 hours, the thickness of the wing web was measured (to the nearest 0.01mm) three times and PHA, which is the responsive swelling, was calculated as the difference between the average thickness before and after injection. This procedure was carried out from 2003 to 2007 (except in 2004). A higher PHA reflects a stronger T-cell mediated response and is a measure of innate immunity (Smits et al. 1999). When nestlings were 16 days old, their tarsus length was measured with a sliding caliper (0.1mm accuracy) and they were weighed using a spring balance (accuracy 0.1g).

Their wing length was measured using a ruler (1mm accuracy) and then one middle tail feather was pulled. Nestlings were sexed using molecular markers (see Brommer & Kluen 2012).

Spectrometry

Reflectance was measured in the lab using a spectrometer (Avantes AvaSpec-2048-SPU2) and a deuterium-halogen light source (AvaLight-DH-S). The light source and the probe were maintained at a 90° angle. Reflectance of the blue in the tail feather of offspring was measured just where the feather vane comes out of the blood shaft of the feather. Because this spot is rather small in nestlings and can be missed by the incident light beam, we measured its reflectance five times. Each spectra was smoothed using a $\pm 10\text{nm}$ running average and we discarded measurements where reflectance did not decrease between 320 and 600nm, which is the general pattern observed for tail structural coloration (see Johnsen et al. 2003 and Figure S1). Feathers collected in 2005 and 2006 were measured in 2006-2007 (University of Jyväskylä, spectrophotometer 1) while the rest of the feathers (2003, 2007-2009) was measured in 2009-2010 (University of Turku) on a different spectrometer of the same model (spectrophotometer 2). Spectra obtained from these two spectrometers have different averages (Figure S1), which was accounted for statistically in further analyses. We used reflectance values measured between 320 and 600 nm in the calculations of the following metrics of coloration: (1) Brightness was quantified as the total reflectance of the feather, (2) hue was calculated as the wavelength of maximum reflectance and (3) UV chroma as the proportion of the total reflectance comprised between 320 and 400nm. Sample sizes (number of individuals and broods), means and standard deviations for each trait are provided in Table 1 and their distribution is plotted in Figure S2. The length of the vane of the feather was measured using a sliding caliper and was used as a covariate in all analyses.

Quantitative genetic analyses

The pruned pedigree (including all phenotyped individuals and up to 3 generations of unphenotyped links between them) was obtained using the function trimPed from the R package “pedigree” (Coster 2012) and was analyzed using the R package “pedantics” (Morrissey 2018). It holds records for 3652 individuals, of which 671 are founders. Mean maternal and paternal sibship sizes are 10.1 and 10.5 respectively, with 2950 dams and 2709 sires. This pedigree was collected over multiple generations, with a maximum pedigree depth of 5 generations, and 2592 grandparents. All nestlings hatched in a nest were assumed to be sired by their social father. Extra-pair paternity in this population is not known but is probably within the range of what was found in other populations (7-25%, Brommer et al. 2010). This level of extra-pair paternity is likely to cause little error in the estimation of quantitative genetic parameters (Charmantier & Réale 2005). There was phenotypic data for 430 genetic broods and on average 69% of them (65%-89%) were reciprocally cross-fostered each year during 2005–2009. Broods from 2003 were not cross-fostered but represent less than 5% of all broods, which is unlikely to affect our estimates of quantitative genetic (co) variances.

We first estimated additive genetic variance for tail brightness, hue, UV chroma, PHA, body mass, and wing length separately using univariate animal models. An animal model is a form of mixed model which allows partitioning phenotypic variance into variance due to additive genetic effects and other sources of variation, using information on the relatedness between individuals derived from the population pedigree (Wilson et al. 2009). This model is noted:

$$y = X\beta + Z_A\mathbf{u}_A + Z_{CE}\mathbf{u}_{CE} + \boldsymbol{\varepsilon} \quad (1)$$

Where \mathbf{y} is a vector containing all observations on all individuals for each trait, β is a vector of fixed effects and X the design matrix relating fixed effects to each individual observation. The vector \mathbf{u}_A , fitted as a random effect, is the vector of additive genetic effects, and its covariance structure is assumed to be proportional to the relatedness matrix Z_A . To account for common

environmental effects occurring when individuals share the same nest, \mathbf{u}_{CE} (and its design matrix \mathbf{Z}_{CE}) was fitted as an additional random effect. Finally, $\boldsymbol{\varepsilon}$ is a vector of residual errors capturing differences between individuals that are unexplained by fixed, additive genetic, and common environment effects. Here, the phenotypic variance (V_P) in performance traits is decomposed into additive genetic variance (V_A), common environment variance (V_{CE}) and residual variance (V_R) as:

$$V_P = V_A + V_{CE} + V_R \quad (2)$$

Because each individual's feather was measured multiple times, an additional individual random effect $\mathbf{Z}_I \mathbf{u}_I$ was fitted to capture among-individual differences in color measures. In these models, the residual component thus captures variation between measurements of the same feather (measurement error). Therefore, the phenotypic variance in color measures is here decomposed into:

$$V_P = V_A + V_{CE} + V_I + V_{ME} \quad (3)$$

Where V_I is the variance between individuals (equivalent to V_R in 2) and V_{ME} the variance in measurement error.

Residuals of all animal models were approximately normally distributed (Shapiro-Wilk test values >0.92 ; Figure S3). Because of visible differences between reflectance measurements made by the two spectrometers (Figure S1 and Table S1), V_{CE} , V_I and V_{ME} of color measures were allowed to vary between these two spectrometers. This was done to assure that our inference of the average additive genetic \mathbf{G} matrix for all nestling traits during the entire study period was accurate.

In all models, sex and year were fitted as categorical fixed effects to account for sexual dimorphism and between-year average differences. Sexes were pooled because cross-sex

genetic correlations for all six traits are high and sex-specific **G** matrices are qualitatively similar (see Tables S2-S10 and Figure S4). The length of the feather vane was fitted as fixed effect covariate for all color measures, and tarsus length was included as a covariate in analyses of nestling's body mass to correct for body size. The animal model was solved using Restricted Maximum Likelihood (REML) and implemented in R (R Development Core Team 2018) using the package "asreml" (Butler et al. 2009). The statistical significance of V_A was tested by comparing each model with a model where V_A was not estimated, using likelihood ratio tests (LRT) with one degree of freedom. Heritability was calculated as the ratio V_A/V_P where V_P did not include V_{ME} for color measures. Uncertainty of this ratio was calculated using the delta method (Fischer et al. 2004).

To partition the covariances between traits into different components, we used a multivariate animal model, in which performance traits and individual averages of each color measure were all fitted as response variables. Using individual averages for the color traits only reduces V_{ME} and does not alter the estimation of V_A . Random effects fitted in this model therefore only included additive genetic effects, common environment effects and residual errors. Fixed effects were similar to the ones used in univariate animal models, some being trait-specific. Covariances on the additive genetic level were tested individually by comparing the unconstrained models to models where these covariances were fixed to zero using LRT, with 1 degree of freedom. The estimated **G** matrix provides 15 estimates of genetic correlations between all six traits. R code for quantitative genetic analyses is provided in Text S1.

Structural equation models

We performed structural equation models (SEM) to reduce the dimensionality of the **G** matrix and investigate the general relationship between each color trait and performance. To do so, **G** matrix estimated by the six-trait animal model was first transformed into a correlation matrix

and used as input data into different SEMs. All performance traits were reduced to a latent factor named “performance” on which they loaded positively. In these models, the variances of “performance” and of each color trait were fixed to 1. Because a correlation matrix was used as input data, the residual variance of each indicator (here, each performance trait), which is the variance unexplained by the latent factor, was fixed to 1 minus its squared factor loading. Each SEM was fitted in R using the package “lavaan” (Rosseel 2012). Sample size in these models was set at 306 as this was the number of nestlings with at least 1 trait measured ($n=3240$) divided by the average paternal sibship size (10.6) and thus approximates the number of families. The sample size in a SEM will not affect the inferred loadings or correlations between latent variables but impacts their uncertainty. In order to take forward the uncertainty of the **G** matrix estimates into the SEM estimates, we calculated 95% confidence intervals (CI) of these correlations using simulation. We first simulated phenotypic data based on the population pedigree and the estimated **G** matrix using the R package “pedantics”. Each simulated data set was analyzed using a multivariate animal model and the estimated **G** matrix was used as input data in a SEM. Only SEM models in which all loadings of performance traits were > 0.05 were kept and simulations were run until obtaining 1000 estimate of correlations between each color trait and performance. This procedure excluded models in which either one loading of a performance trait on “performance” or the correlation between color and performance were abnormally high (>10) while the (other) loadings were zero. This situation occurred under certain values of the **G** matrix (e.g. when low correlations switch signs) and thus, SEM estimates based on these values were discarded. As a result, the 95% CI of the average correlation between color traits and performance may not have fully incorporated the uncertainty of the **G** matrix and should not be interpreted as a test for statistical significance. R code for performing SEMs and simulations are provided in Text S2 and Text S3.

Results

241 All tail color and performance traits were measured in over 2800 nestlings, except the PHA
 242 response, which was measured on fewer nestlings (Table 1). Measurement repeatability of tail
 243 color was significant, although relatively low (40-50% for brightness and UV chroma; around
 244 30% for hue, Table S1) compared to measurement repeatability of adult color in other blue tit
 245 populations (e.g. Doutrelant et al. 2008, Figuerola et al. 1999). There was significant sexual
 246 dimorphism in these nestlings for all tail color measures but also for mass and wing length
 247 (Table S11-S16).

248 Heritability of tail color measures was low (1-12%, Table 2). These color measures were
 249 negatively but not significantly correlated with each other on the genetic level (trivariate model:
 250 UV chroma-brightness: $r_G = -0.17$, $se = 0.36$), $\chi^2_1 = 0.07$, $p = 0.78$; hue-brightness: $r_G = -0.75$,
 251 $se = 0.45$, $\chi^2_1 = 2.50$, $p = 0.11$; hue-UV chroma: $r_G = -0.34$, $se = 0.54$, $\chi^2_1 = 0.37$, $p = 0.54$; Table 3). We
 252 hence studied color traits independently in further analyses. In contrast, heritability estimates
 253 of performance traits (body mass, wing length, and PHA response) were all moderate (19-28%,
 254 Table 2). Heritability of PHA using repeated measures of nestlings' wing web before and after
 255 injection was also calculated (excluding measurement error) using a bivariate animal model and
 256 was close to the estimate based on individual averages ($h^2 = 0.16$, $se = 0.04$; Table S17).

257 All performance traits were positively correlated on the genetic level (trivariate model: PHA-
 258 body mass: $r_G = 0.61$, $se = 0.04$, $\chi^2_1 = 53.1$, $p < 0.001$; wing-PHA: $r_G = 0.36$, $se = 0.07$, $\chi^2_1 = 30.5$,
 259 $p < 0.001$; body mass-wing: $r_G = 0.46$, $se = 0.07$, $\chi^2_1 = 408.0$, $p < 0.001$; Table 3). These correlations
 260 were not affected by the nestlings' wing web thickness before injection (PHA- body mass:
 261 $r_G = 0.59$, $se = 0.04$; wing-PHA: $r_G = 0.36$, $se = 0.07$; body mass-wing: $r_G = 0.43$, $se = 0.06$).
 262 (Co)Variance matrices are all reported in the electronic supplementary material (Tables S18-
 263 S22).

Regarding genetic correlations between coloration and performance traits, inspection of the **G** matrix (highlighted part in Table 3) shows that UV chroma is consistently negatively correlated with performance traits. In contrast, the signs of the genetic correlations between the two other color measures and performance traits are inconsistent. Separate SEMs were run for each color trait independently, to estimate its average correlation with performance. These analyses indicated that tail brightness was (largely) positively (coefficient = 0.39; 95% CI = -0.09–1.00), and UV chroma negatively (coefficient = -0.69; 95% CI = -1.36–-0.15) correlated with performance. For hue, this correlation was weakly negative (coefficient = -0.12; 95% CI = -0.81–0.40, Figure S5).

Discussion

In this study, we used long-term nestling data, pedigree information and a cross-fostering design to estimate additive genetic variation in coloration measures, performance traits and genetic correlations between them, and find evidence for indirect benefits of blue tail coloration in wild blue tits.

Tail color measures had a low heritability which is in line with other heritability estimates of carotenoid and structural coloration in blue tits (Evans & Sheldon 2012, Hadfield et al. 2006, Drobniak et al. 2013, Charmantier et al. 2017). In contrast, heritability of performance traits (body mass, wing length, and PHA response) was generally moderate and within the range of what was found in other populations or species (see e.g. Merilä & Sheldon 2000, Merilä et al. 2001, Hadfield et al. 2007 for morphometric traits, and Pitälä et al. 2007, Kim et al. 2013 for PHA response). In addition all performance traits were positively correlated on the genetic level, which is consistent with previous estimates of genetic correlations between mass and wing length (e.g. Björklund et al. 2013) and between mass and PHA response (Kim et al. 2013) and indicates the presence of additive genetic variation for individual performance. Using

SEMs, we found that the average genetic correlation between each color measure and a latent factor “performance”, was positive for tail brightness, negative for UV chroma, and weakly negative for hue.

Hence, our findings suggest indirect fitness benefits of choosing mates with tails that are brighter or reflecting less in the UV. Indeed, all three performance traits are known to be positively associated with fitness. While the positive effects of mass at fledging on survival have been well documented (e.g. Perrins 1965, Tinbergen & Boerlijst 1990, Lindén et al. 1992, Radersma et al. 2015), wing length was shown to determine fledging date (Radersma et al. 2011), and impact recruitment probability (Verboven & Visser 1998), possibly through competitive advantage or decreased predation risk. PHA can also be considered an important functional trait as it was shown to increase survival and recruitment probability of nestlings in various species (Hörak et al. 1999, Moreno et al. 2005, Cichoń & Dubiec 2005, López-Rull et al. 2011), although this relationship may be due to its condition-dependence (Alonso-Alvarez & Tella 2001, Thompson et al. 2014). Nevertheless, PHA, body mass and wing length were heritable and genetically correlated, which suggests that their genetic architecture “captures the so-called good genes” and allow sexual selection for indirect benefits to occur in this population. Because tail color indicates immune response through its genetic relationship with performance, our results also support the PMSS hypothesis.

Previous studies showed that bluer plumage ornaments are condition-dependent in juveniles (Johnsen et al. 2003, Jacot & Kempenaers 2007, Peters et al. 2007 in blue tits, Siefferman et al. 2008, Siefferman & Hill 2007 in other species) and in adults (Doutrelant et al. 2012, Beck et al. 2015, Galván 2011), which contrasts with the negative genetic association that we found between hue, UV chroma, and performance traits. Importantly, correlations between hue, UV chroma and performance traits were also negative on the phenotypic level (Table S23). This negative relationship implies that developing bluer tails early in life has costs which can impact

individuals' probability to recruit. However, these fitness costs may be offset on the first reproductive year, if yearlings with a bluer tail are sexually more attractive than duller yearlings. On the other hand, genetic correlations between hue, UV chroma and performance should be interpreted with caution given the very low heritability of both color measures and the high uncertainty of their additive genetic variance estimates.

In the context of sexual selection based on indirect benefits, key parameters are the (square root) heritability of the sexually selected trait, additive genetic variance in fitness and genetic correlation between this trait and fitness (Kirkpatrick and Barton 1997). This means that, for mate choice based on indirect benefits of an ornament to evolve, this ornament has to provide sufficient information regarding an individual's genotype. Because we found low heritability for tail color measures, our results imply that indirect sexual selection on mate choice for this ornament will be a weak evolutionary force (cf. Møller & Alatalo 1999, Qvarnström et al. 2006).

Despite broad interest in understanding the evolution of animal ornaments, studies estimating heritability of coloration and its genetic correlation with performance to test the indirect benefits hypothesis remain rare. This study provides evidence for additive genetic variation in tail coloration and performance and for a genetic association between them. More specifically, our findings suggest that mate choice based on tail brightness and UV chroma can have fitness payoffs in blue tits and hence support indirect benefits of mate choice for this ornament. However, because of the low heritability of tail structural coloration, this mechanism may not be a major driver of its evolution.

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524 **Supporting information**

525

526 **Table S1:** Repeatability of each color trait measured by each spectrometer

527 **Figure S1:** Average reflectance spectrum measured by each spectrometer

528 **Figure S2:** Distribution of the six traits measured in nestlings

529 **Figure S3:** Distribution of the univariate animal model residuals for all six traits

530 **Tables S2-S7:** Sex-specific variances and cross-sex covariances estimated by bivariate animal
531 models for each trait separately

532 **Figure S4:** Additive genetic variances of all six traits and their covariances in males and females

533 **Tables S8-S9:** Genetic correlation matrix estimated by a multivariate mixed model in females
534 and males respectively.

535 **Table S10:** Cross-sex genetic correlation and SE for each trait

536 **Tables S11-S16:** Fixed and random effects estimated by the animal model for each trait

537 **Tables S17:** Variances of wing web thickness measured on day 13 and day 14 and their
538 covariances estimated on different levels by a bivariate animal model

539 **Tables S18-S22:** Covariance matrices derived from the multivariate animal model

540 **Figure S5:** Correlations and loadings estimated in the structural equation models

541 **Tables S23:** Phenotypic correlation matrix derived from a multivariate mixed model

542 **Text S1:** R code for performing quantitative genetic analyses

543 **Text S2-S3:** R code for performing structural equation modelling and simulations

Table 1: Number of individuals, rearing broods, mean and standard deviation (SD) for each studied trait.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
n.individuals	2851	2851	2851	1516	3210	3200
n.broods	364	364	364	173	390	389
mean (SD)	9.46 (2.74)	340.78 (10.61)	0.33 (0.02)	0.54 (0.17)	11.40 (1.08)	46.34 (3.39)

Table 2: Animal model estimates (and standard errors) of variance components of all six traits. Heritability (h^2) and ratio V_{CE}/V_P (and their standard error) were calculated for each trait, where V_P is the sum of all estimated variances, except for color traits where it does not include V_{ME} . For tail color traits, V_I , V_{CE} and V_{ME} were estimated separately for each spectrophotometer used (1 and 2 respectively) and thus two h^2 and ratios V_{CE}/V_P were calculated.

		Brightness	Hue	UV chroma	PHA	Body mass	Wing
V_A		0.26 (0.13)	1.2 (2.02)	6.24E-06 (3.93E-06)	5.17E-06 (1.36E-03)	0.25 (0.04)	3.26 (0.46)
V_{CE}	1	0.94 (0.19)	11.39 (2.52)	1.63E-05 (3.54E-06)	7.83E-06 (1.21E-06)	0.49 (0.04)	4.87 (0.57)
	2	1.68 (0.21)	24.11 (3.06)	1.35E-04 (1.78E-05)			
V_I	1	1.43 (0.16)	19.66 (2.76)	2.84E-05 (3.79E-06)	1.30E-02 (1.02E-03)	0.19 (0.02)	3.46 (0.35)
	2	2.89 (0.17)	40.32 (2.75)	3.32E-04 (1.58E-05)			
V_{ME}	1	2.32 (0.06)	82.47 (2.12)	4.83E-05 (3.24E-06)			
	2	6.55 (0.11)	122.6 (2.06)	5.51E-04 (9.25E-06)			
V_R							
h^2	1	0.10 (0.05)	0.04 (0.06)	0.12 (0.08)	0.19 (0.06)	0.27 (0.04)	0.28 (0.05)
	2	0.05 (0.03)	0.02 (0.03)	0.01 (0.008)			
V_{CE}/V_P	1	0.36 (0.05)	0.35 (0.06)	0.32 (0.05)	0.30 (0.04)	0.52 (0.02)	0.42 (0.03)
	2	0.35 (0.03)	0.37 (0.03)	0.29 (0.03)			

Table 3: Additive genetic correlation (and standard error) matrix estimated by the multivariate animal model. Correlations between color measures and performance traits are highlighted in grey.

Brightness	Hue	UV chroma	PHA	Body mass	Wing
-0.72 (0.40)					
-0.13 (0.41)	-0.34 (0.54)				
-0.05 (0.25)	-0.04 (0.30)	-0.50 (0.33)			
0.21 (0.20)	0.13 (0.23)	-0.17 (0.28)	0.23 (0.16)		
0.50 (0.24)	-0.51 (0.28)	-0.35 (0.35)	0.32 (0.19)	0.26 (0.13)	

Supplementary material belonging to the article

“Tail color signals performance in blue tit nestlings”

Table S1: Repeatability of each color measured by each spectrometer

Trait	Repeatability 1 (95% CI)	Repeatability 2 (95% CI)
brightness	0.51 (0.48-0.55)	0.40 (0.38-0.43)
hue	0.28 (0.32-0.25)	0.33 (0.31-0.36)
UV chroma	0.50 (0.47-0.54)	0.43 (0.41-0.45)

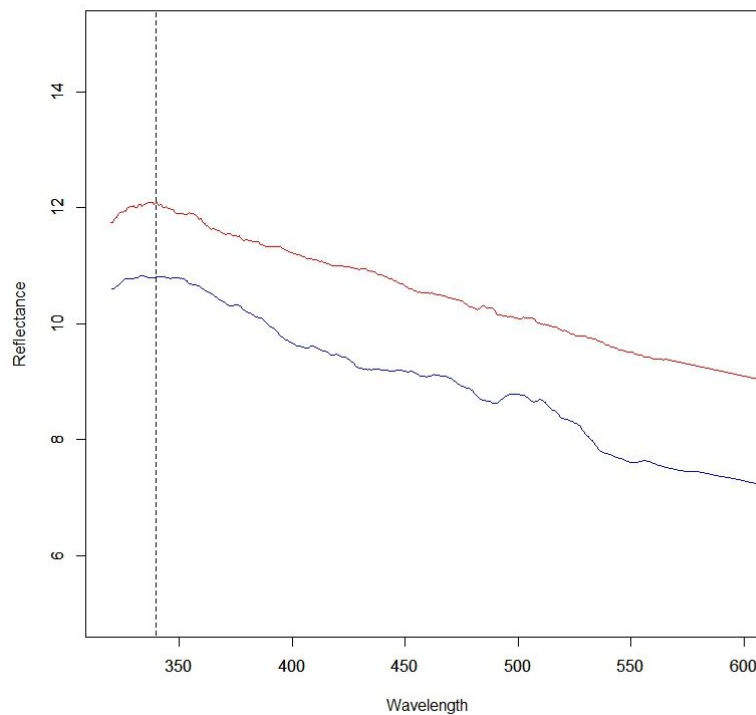
Figure S1: Average reflectance spectra from nestlings’ tail feathers in 2005-2006 (first spectrometer, red line), and in 2003+2007-2009 (second spectrometer, blue line). The dotted vertical line represents the peak reflectance for both spectrophotometers.

Figure S2: Distribution of the six traits (averages per individual) measured in nestlings.

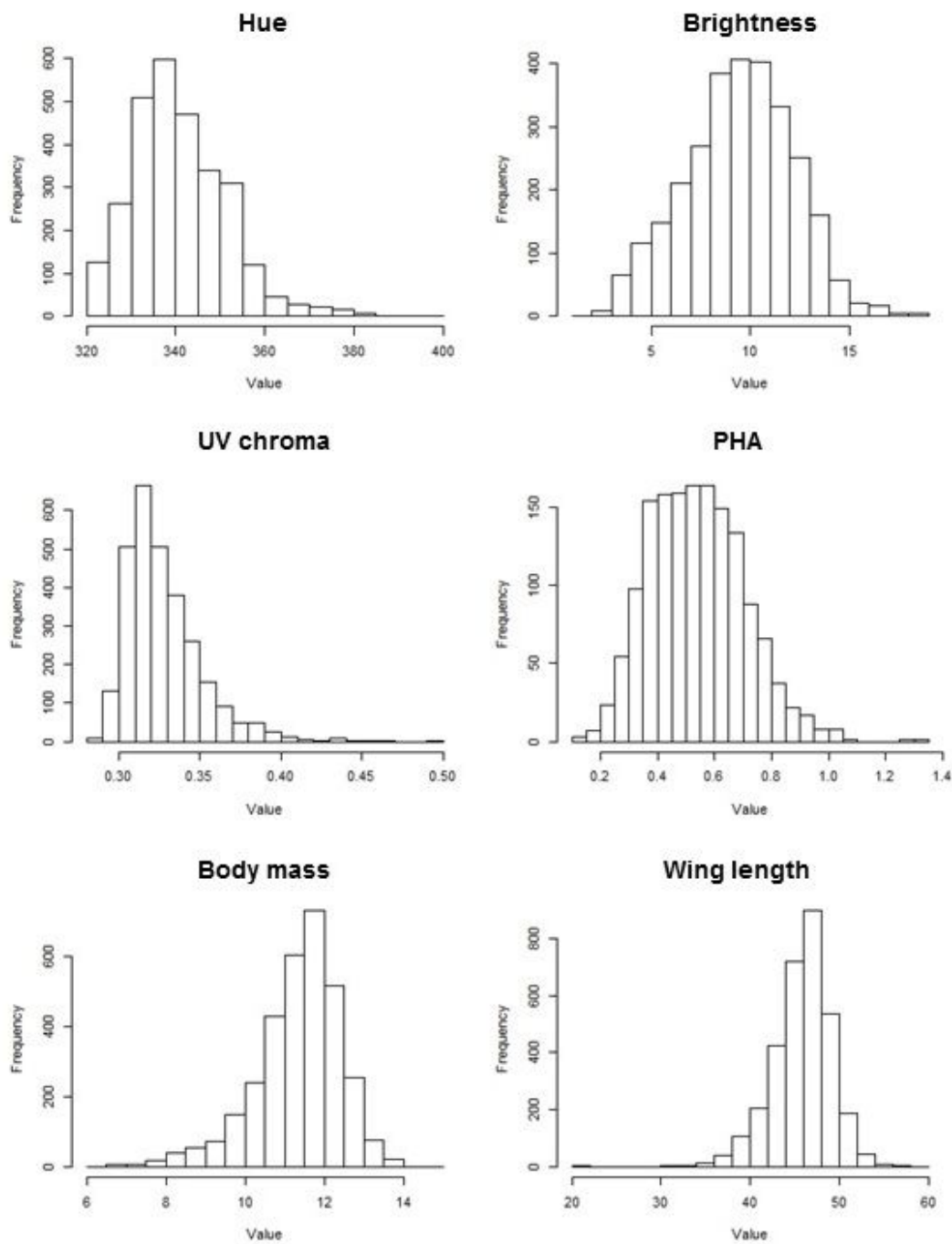


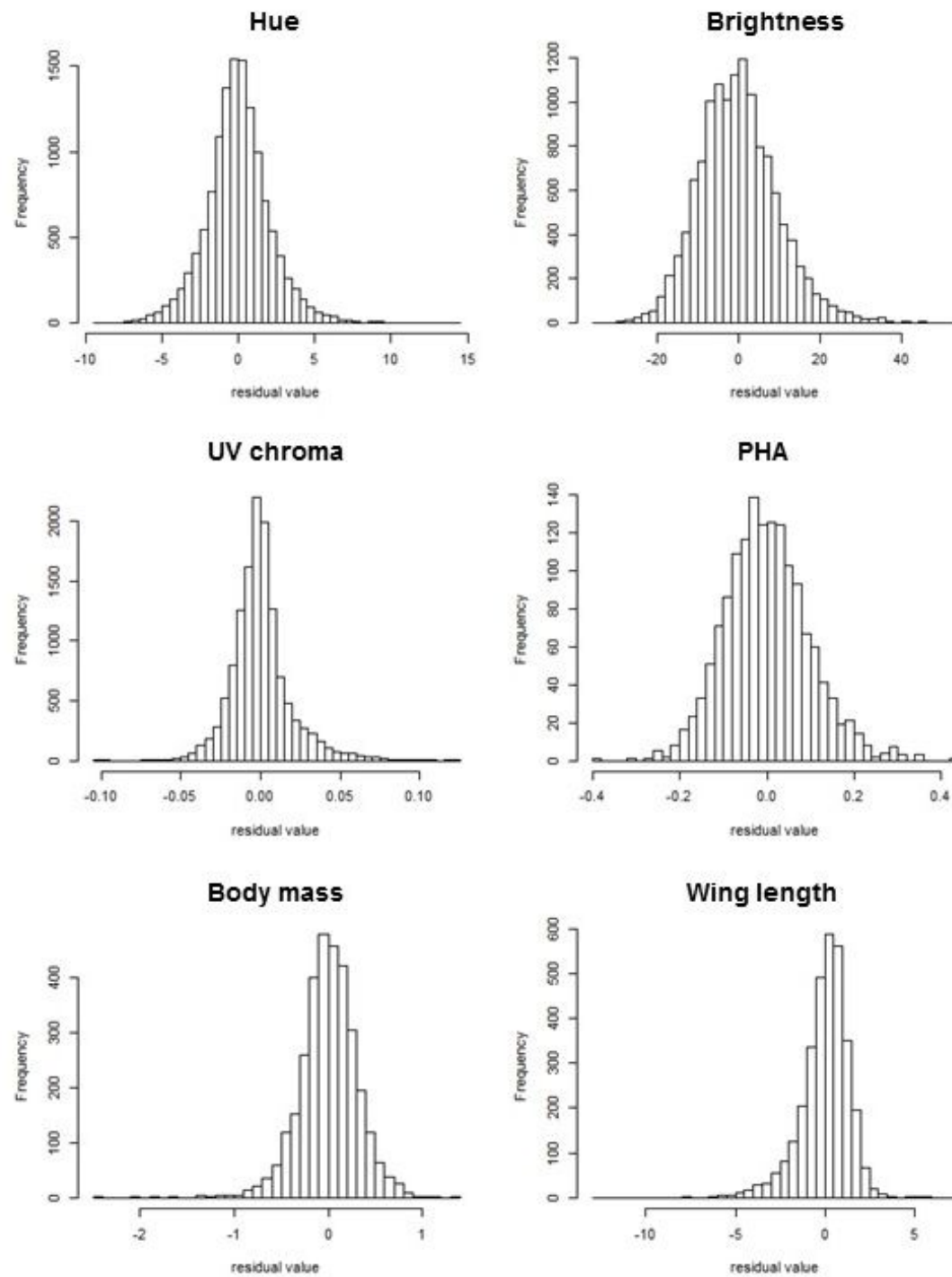
Figure S3: Distribution of the univariate animal model residuals for all six traits

Table S2: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with tail brightness in males and in females as two response variables. Common environment and residual error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Component	Parameter	Estimate	SE	z.ratio
Common environment 1	V_m	1.12	0.26	4.40
	COV_{mf}	0.90	0.20	4.49
	V_f	0.78	0.23	3.35
Common environment 2	V_m	1.50	0.27	5.60
	COV_{mf}	1.68	0.24	6.99
	V_f	2.00	0.34	5.85
Additive genetic	V_m	0.22	0.19	1.21
	COV_{mf}	0.31	0.17	1.85
	V_f	0.45	0.29	1.56
Residual 1	V_m	1.65	0.21	7.76
	V_f	2.08	0.31	6.72
Residual 2	V_m	4.36	0.26	16.57
	V_f	4.89	0.33	14.94

Table S3: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with tail hue in males and in females as two response variables. Common environment and residual error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Component	Parameter	Estimate	SE	z.ratio
Common environment 1	V_m	11.81	4.17	2.83
	COV_{mf}	12.38	3.38	3.67
	V_f	17.87	4.69	3.81
Common environment 2	V_m	29.72	4.96	5.99
	COV_{mf}	24.48	3.78	6.48
	V_f	20.29	4.68	4.34
Additive genetic	V_m	4.96	4.96	1.00
	COV_{mf}	4.94	4.00	1.24
	V_f	14.25	5.58	2.56
Residual 1	V_m	49.27	6.09	8.09
	V_f	25.05	5.32	4.71
Residual 2	V_m	71.25	4.96	14.36
	V_f	80.45	5.79	13.90

Table S4: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with tail UV chroma in males and in females as two response variables. Common environment and residual error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Component	Parameter	Estimate	SE	z.ratio
Common environment 1	V_f	1.26E-05	3.95E-06	3.20
	COV_{mf}	1.67E-05	3.83E-06	4.35
	V_m	2.20E-05	5.62E-06	3.91
Common environment 2	V_f	1.34E-04	2.64E-05	5.07
	COV_{mf}	1.43E-04	2.09E-05	6.84
	V_m	1.58E-04	2.65E-05	5.96
Additive genetic	V_f	1.21E-05	7.45E-06	1.63
	COV_{mf}	1.21E-05	5.75E-06	2.11
	V_m	1.22E-05	8.14E-06	1.50
Residual 1	V_f	2.75E-05	6.23E-06	4.42
	V_m	3.63E-05	6.98E-06	5.20
Residual 2	V_f	5.02E-04	2.70E-05	18.58
	V_m	4.29E-04	2.32E-05	18.53

Table S5: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with PHA in males and in females as two response variables.

Component	Parameter	Estimate	SE	z.ratio
Common environment	V_f	6.16E-03	1.38E-03	4.45
	COV_{mf}	7.54E-03	1.29E-03	5.85
	V_m	9.88E-03	1.71E-03	5.77
Additive genetic	V_f	7.47E-03	2.15E-03	3.47
	COV_{mf}	5.71E-03	1.57E-03	3.64
	V_m	4.49E-03	1.90E-03	2.37
Residual	V_f	1.15E-02	1.60E-03	7.22
	V_m	1.30E-02	1.56E-03	8.31

Table S6: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with body mass in males and in females as two response variables.

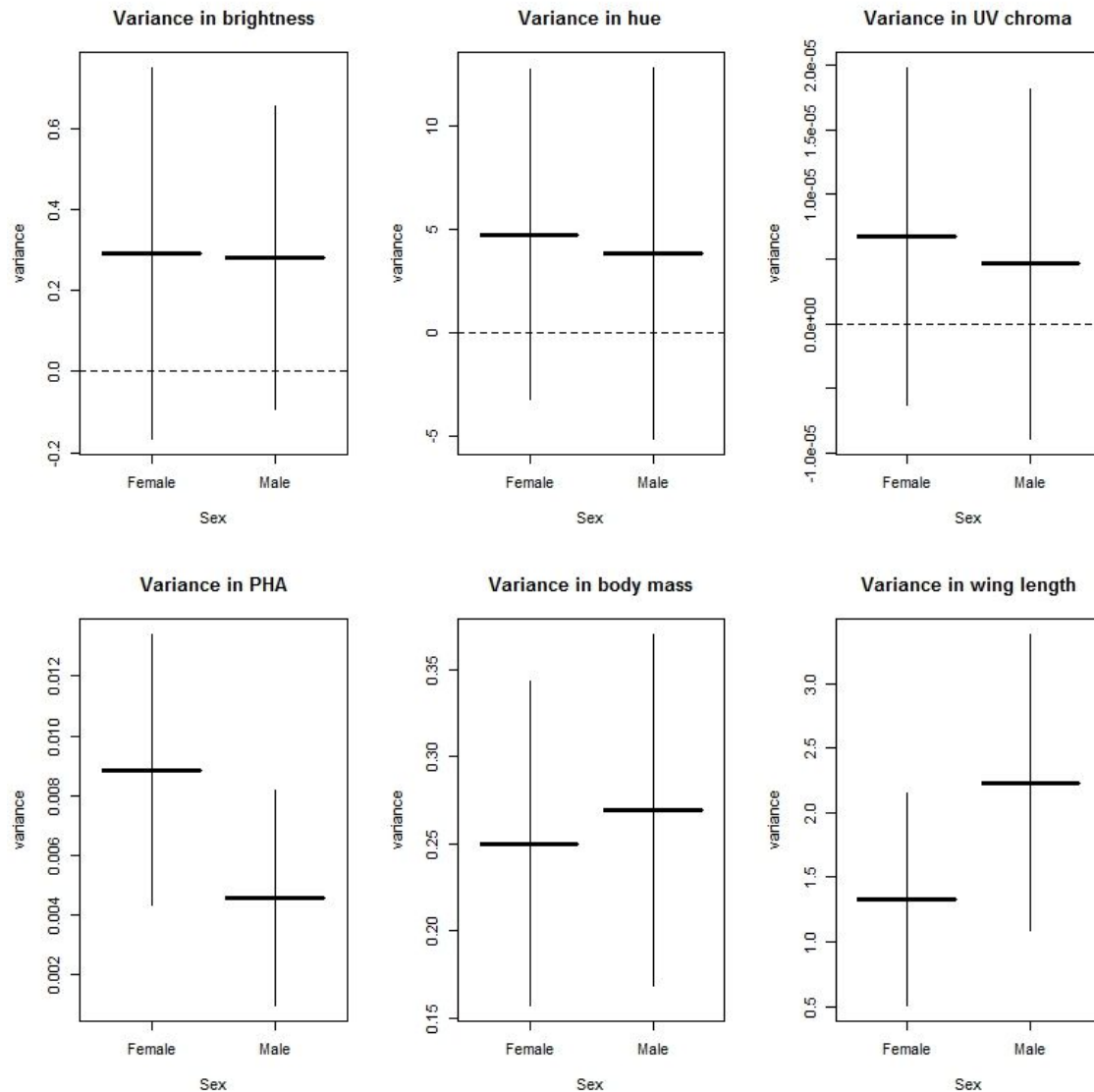
Component	Parameter	Estimate	SE	z.ratio
Common environment	V_f	0.44	0.04	10.25
	COV_{mf}	0.43	0.04	11.08
	V_m	0.43	0.04	10.02
Additive genetic	V_f	0.24	0.04	5.69
	COV_{mf}	0.24	0.04	6.44
	V_m	0.28	0.05	6.09
Residual	V_f	0.15	0.03	5.65
	V_m	0.17	0.03	5.83

Table S7: Variances and covariances, their standard error (SE), and z ratio, estimated by a bivariate animal model with wing length in males and in females as two response variables.

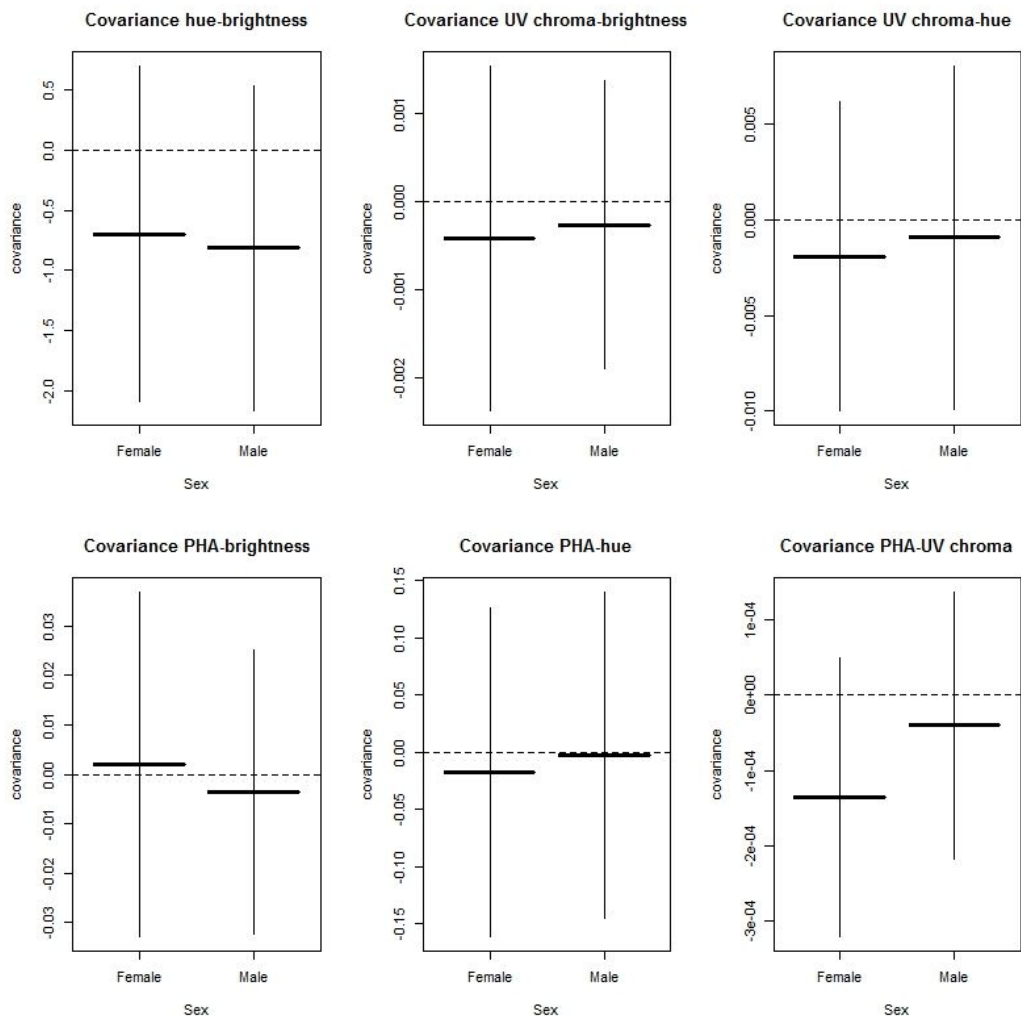
Component	Parameter	Estimate	SE	z.ratio
Common environment	V_f	4.94	0.50	9.81
	COV_{mf}	4.79	0.46	10.47
	V_m	5.08	0.53	9.53
Additive genetic	V_f	1.86	0.47	4.00
	COV_{mf}	2.02	0.44	4.60
	V_m	2.46	0.61	4.03
Residual	V_f	3.31	0.33	9.94
	V_m	3.89	0.43	8.97

Figure S4: A) Additive genetic variances and their 95%CI in both sexes for all six traits and **B)** additive genetic covariances between these traits. These (co)variances and their uncertainties were estimated by a multivariate animal model for each sex separately.

A) Variances



B) Covariances (part 1)



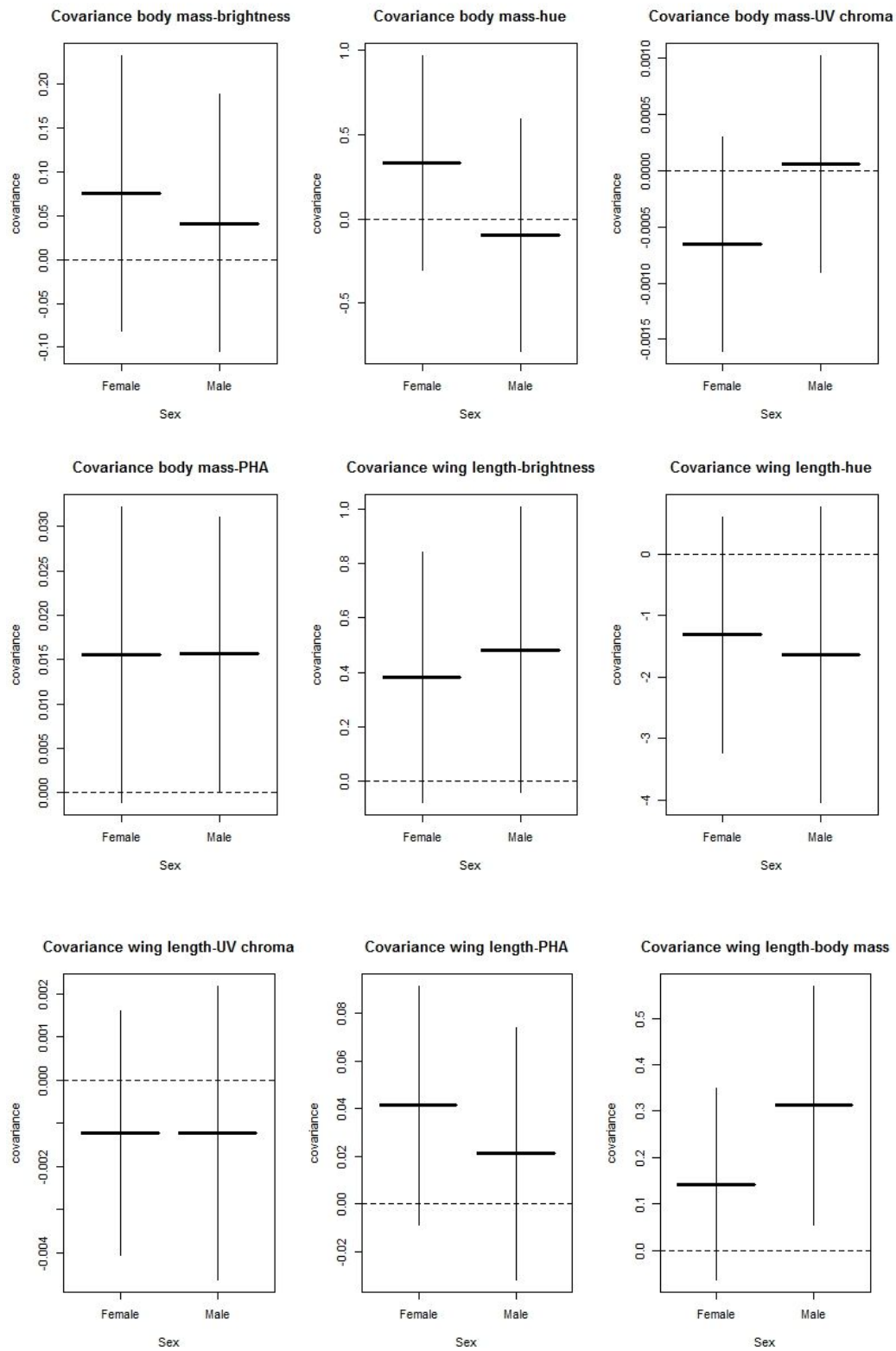
B) Covariances (part 2)

Table S8: Genetic correlation matrix estimated by a multivariate mixed model **in females**. In this model, fixed effects were similar to fixed effects fitted in the multivariate animal model and only the residual component was estimated. Correlations (and their standard error) are in the lower triangle and the diagonal (underlined numbers) contains phenotypic variances (and their standard error) estimated by the model. Correlations between color measures and performance traits are highlighted in grey.

Brightness	Hue	UV chroma	PHA	Body mass	Wing
-0.59 (0.61)					
-0.30 (0.71)	-0.33 (0.73)				
0.04 (0.35)	-0.09 (0.36)	-0.55 (0.38)			
0.28 (0.30)	0.30 (0.30)	-0.50 (0.37)	0.33 (0.18)		
0.61 (0.38)	-0.52 (0.39)	-0.40 (0.48)	0.38 (0.24)	0.25 (0.18)	

Table S9: Genetic correlation matrix estimated by a multivariate mixed model **in males**. In this model, fixed effects were similar to fixed effects fitted in the multivariate animal model and only the residual component was estimated. Correlations (and their standard error) are in the lower triangle and the diagonal (underlined numbers) contains phenotypic variances (and their standard error) estimated by the model. Correlations between color measures and performance traits are highlighted in grey.

Brightness	Hue	UV chroma	PHA	Body mass	Wing
-0.79 (0.67)					
-0.24 (0.73)	-0.22 (1.09)				
-0.10 (0.41)	-0.02 (0.55)	-0.28 (0.62)			
0.15 (0.27)	-0.10 (0.35)	0.05 (0.44)	0.45 (0.23)		
0.61 (0.34)	-0.56 (0.42)	-0.38 (0.54)	0.21 (0.27)	0.4 (0.17)	

Table S10: Cross-sex genetic correlation and SE for each trait

Trait	R _{g_{mf}}	SE
Brightness	0.99	0.53
Hue	0.59	0.48
UV chroma	0.95	0.52
PHA	0.98	0.17
Body mass	0.92	0.05
Wing length	0.94	0.08

Table S11: Fixed and random effects (and their standard error SE) estimated by the animal model for tail brightness. The statistical significance of additive genetic variance was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter. Common environment, individual, and measurement error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment 1	0.94	0.19		
Common environment 2	1.68	0.21		
Additive genetic	0.26	0.13	$\chi^2=6.19$	0.01
Individual 1	1.43	0.16		
Individual 2	2.89	0.17		
Measurement error 1	2.32	0.06		
Measurement error 2	6.55	0.11		
Fixed effects				
Intercept	6.85	0.44	$F_{1,287.2}=842.20$	<0.001
Vane	0.28	0.02	$F_{1,1894.0}=324.60$	<0.001
Year			$F_{5,287.63}=36.18$	<0.001
2005	1.15	0.48		
2006	-0.65	0.47		
2007	-1.91	0.49		
2008	-0.60	0.47		
2009	-1.70	0.47		
Sex			$F_{2,2308.1}=9.58$	<0.001
female	0.16	0.20		
male	-0.18	0.20		

Table S12: Fixed and random effects (and their standard error SE) estimated by the animal model for tail hue. The statistical significance of additive genetic variance was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter. Common environment, individual, and measurement error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment 1	11.39	2.52	$\chi^2=0.20$	0.65
Common environment 2	24.11	3.06		
Additive genetic	1.20	2.02		
Individual 1	19.66	2.76		
Individual 2	40.32	2.75		
Measurement error 1	82.47	2.12		
Measurement error 2	122.60	2.06		
Fixed effects				
Intercept	354.16	1.68	$F_{1,219.7}=1.89E+05$	<0.001
Vane	-0.44	0.06	$F_{1,1629.8}=52.1$	<0.001
Year			$F_{5,283.7}=24.09$	<0.001
2005	-4.93	1.82		
2006	-10.89	1.79		
2007	-10.28	1.85		
2008	-9.79	1.79		
2009	-4.65	1.79		
Sex			$F_{2,2387.1}=5.98$	0.002
female	-0.42	0.79		
male	-1.43	0.78		

Table S13: Fixed and random effects (and their standard error SE) estimated by the animal model for tail UV chroma. The statistical significance of additive genetic variance was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter. Common environment, individual, and measurement error variances were estimated separately for each spectrophotometer (1: feathers from 2005-2006, 2: feathers from 2003, 2007-2009).

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment 1	1.63E-05	3.54E-06	$\chi^2=4.31$	0.04
Common environment 2	1.35E-04	1.78E-05		
Additive genetic	6.24E-06	3.93E-06		
Individual 1	2.84E-05	3.79E-06		
Individual 2	3.32E-04	1.58E-05		
Measurement error 1	4.83E-05	1.24E-06		
Measurement error 2	5.51E-04	9.25E-06		
Fixed effects				
Intercept	3.32E-01	3.85E-03	$F_{1,149.6}=72020.00$	<0.001
Vane	-3.58E-04	8.97E-05	$F_{1,779.1}=15.92$	<0.001
Year			$F_{5,295.7}=66.67$	<0.001
	2005	-1.74E-02	3.95E-03	
	2006	-1.30E-02	3.93E-03	
	2007	9.45E-03	4.29E-03	
	2008	1.79E-03	4.14E-03	
	2009	6.58E-05	4.10E-03	
Sex			$F_{2,1083.4}=157.10$	<0.001
	female	-1.93E-03	1.20E-03	
	male	6.10E-03	1.19E-03	

Table S14: Fixed and random effects (and their standard error SE) estimated by the animal model for PHA response. The statistical significance of random effects was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter.

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment	7.83E-03	1.21E-03	$\chi^2=153.09$	<0.001
Additive genetic	5.17E-03	1.36E-03	$\chi^2=46.48$	<0.001
Residual	1.30E-02	1.02E-03		
Fixed effects				
Intercept	0.49	0.03	$F_{1,196.7} = 3920.0$	<0.001
Year			$F_{3,207.9} = 6.52$	<0.001
	2005	0.04		
	2006	0.06		
	2007	-0.02		
Sex			$F_{1,1422.8} = 1.69$	0.85
	female	0.035		
	male	0.037		

Table S15: Fixed and random effects (and their standard error SE) estimated by the animal model for body mass. The statistical significance of random effects was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter.

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment	0.49	0.04	$\chi^2=1093.62$	<0.001
Additive genetic	0.25	0.04	$\chi^2=185.67$	<0.001
Residual	0.19	0.02		
Fixed effects				
Intercept	8.51	0.27	$F_{1,494.3} = 2401.00$	<0.001
Tarsus	0.13	0.01	$F_{1,3107.0} = 184.50$	<0.001
Year			$F_{5,404.4} = 12.95$	<0.001
2005	0.42	0.24		
2006	0.68	0.24		
2007	0.17	0.23		
2008	0.85	0.23		
2009	0.92	0.22		
Sex			$F_{1,2928.2} = 213.00$	<0.001
female	-0.27	0.06		
male	0.21	0.06		

Table S16: Fixed and random effects (and their standard error SE) estimated by the animal model for wing length. The statistical significance of random effects was tested using LRT with 1df. The statistical significance of fixed effects was tested using conditional Wald-F tests. Coefficients of years and sex effects are reported as contrasts to year 2003 for the former and to unsexed individuals for the latter.

Effect	Estimate	SE	Test statistic	p.value
Random effects				
Common environment	4.87	0.46	$\chi^2=616.89$	<0.001
Additive genetic	3.26	0.57	$\chi^2=64.74$	<0.001
Residual	3.46	0.35		
Fixed effects				
Intercept	44.56	0.69	$F_{1,435.6} = 97880.00$	<0.001
Year			$F_{5,404.0} = 7.34$	<0.001
2005	1.31	0.82		
2006	2.85	0.80		
2007	0.44	0.77		
2008	1.43	0.77		
2009	0.84	0.76		
Sex			$F_{1,2953.4} = 25.18$	<0.001
female	0.09	0.25		
male	0.72	0.25		

Table S17: Variances of wing web thickness measured on day 13 and day 14 and their covariances estimated on different levels by a bivariate animal model (and their standard errors (SE)). In this model, year and sex were fitted as fixed effects for each response separately and random effects included common environment effects, individual identity, additive genetic effects and measurement error. Measurement error covariance was not fitted as both measures were not taken at the same time. Variance of the PHA response on each level can then be estimated as the sum of both variances minus twice their covariance and heritability is calculated as VA/VP where VP does not include measurement error.

(Co)Variance component	Estimate	SE
Common environment: WingWeb_d13	3.89	0.51
Common environment:WingWeb_d14:WingWeb_d13	7.28	1.25
Common environment: WingWeb_d14	33.77	4.87
Additive genetic: WingWeb_d13	0.52	0.23
Additive genetic: WingWeb_d14:WingWeb_d13	-1.16	0.64
Additive genetic: WingWeb_d14	11.97	3.62
Individual: WingWeb_d13	3.89	0.23
Individual: WingWeb_d14:WingWeb_d13	2.29	0.61
Individual: WingWeb_d14	55.62	3.28
Measurement error: WingWeb_d13	0.71	0.03
Measurement error : WingWeb_d14	3.24	0.08
Common environment: PHA	23.10	3.77
Additive genetic: PHA	14.82	3.98
Individual: PHA	54.94	3.41

Table S18: Additive genetic covariance matrix derived from the multivariate animal model. The diagonal contains additive genetic variances and standard errors are printed below each estimate in grey. Covariances between color measures and performance traits are highlighted in yellow.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
Brightness	0.28 0.12					
Hue	-0.80 0.44	4.44 2.90				
UV chroma	-1.60E-04 4.93E-04	-1.63E-03 2.59E-03	5.19E-06 3.58E-06			
PHA	-1.87E-03 9.72E-03	-0.01 0.05	-8.30E-05 5.47E-05	5.32E-03 1.31E-03		
Body mass	0.05 0.05	0.13 0.23	-1.86E-04 3.04E-04	8.15E-03 5.46E-03	0.23 0.03	
Wing	0.34 0.17	-1.42 0.78	-1.01E-03 1.04E-03	3.05E-02 1.81E-02	0.16 0.08	1.73 0.37

Table S19: First common environment (CE1) covariance matrix derived from the multivariate animal model. The diagonal contains CE1 variances and standard errors are printed below each estimate in grey. Covariances between color measures and performance traits are highlighted in yellow.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
Brightness	1.04 0.21					
Hue	-0.42 0.57	12.93 3.00				
UV chroma	-1.50E-03 6.52E-04	-4.17E-03 2.43E-03	1.74E-05 3.69E-06			
PHA	0.04 0.02	-0.01 0.06	7.64E-05 6.53E-05	1.12E-02 2.18E-03		
Body mass	0.34 0.11	0.31 0.41	9.01E-04 4.58E-04	5.25E-02 0.01	0.60 0.10	
Wing	1.50 0.43	1.21 1.53	1.80E-04 1.70E-03	1.41E-01 0.04	1.18 0.30	7.92 1.40

Table S20: Second common environment (CE2) covariance matrix derived from the multivariate animal model. The diagonal contains CE1 variances and standard errors are printed below each estimate in grey. Covariances between color measures and performance traits are highlighted in yellow.

	Brightness	Hue	UV chroma	PHA	Mass	Wing
Brightness	1.95 0.24					
Hue	-1.52 0.65	25.09 3.43				
UV chroma	-1.16E-02 1.77E-03	-1.74E-02 5.91E-03	1.44E-04 1.84E-05			
PHA	0.01 0.02	3.43E-03 5.84E-02	-1.01E-04 1.30E-04	3.45E-03 9.62E-04		
Mass	0.32 0.08	-0.09 0.29	-2.20E-03 6.70E-04	1.89E-02 6.11E-03	0.46 0.05	
Wing	1.51 0.25	-2.00 0.90	-7.99E-03 2.09E-03	3.65E-03 2.00E-02	0.67 0.11	4.18 0.44

Table S21: First residual (RES1) covariance matrix derived from the multivariate animal model. The diagonal contains RES1 variances and standard errors are printed below each estimate in grey. Covariances between color measures and performance traits are highlighted in yellow.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
Brightness	2.02 0.16					
Hue	-0.02 0.54	45.29 3.61				
UV chroma	-1.75E-03 5.50E-04	-1.01E-02 2.81E-03	4.08E-05 3.73E-06			
PHA	-3.96E-03 1.07E-02	0.03 0.05	1.02E-04 5.30E-05	1.44E-02 1.28E-03		
Body mass	0.01 0.05	-0.19 0.26	6.53E-04 2.75E-04	1.51E-02 4.84E-03	0.27 0.03	
Wing	0.41 0.22	1.53 1.06	3.81E-03 1.14E-03	0.05 0.02	0.72 0.10	7.78 0.54

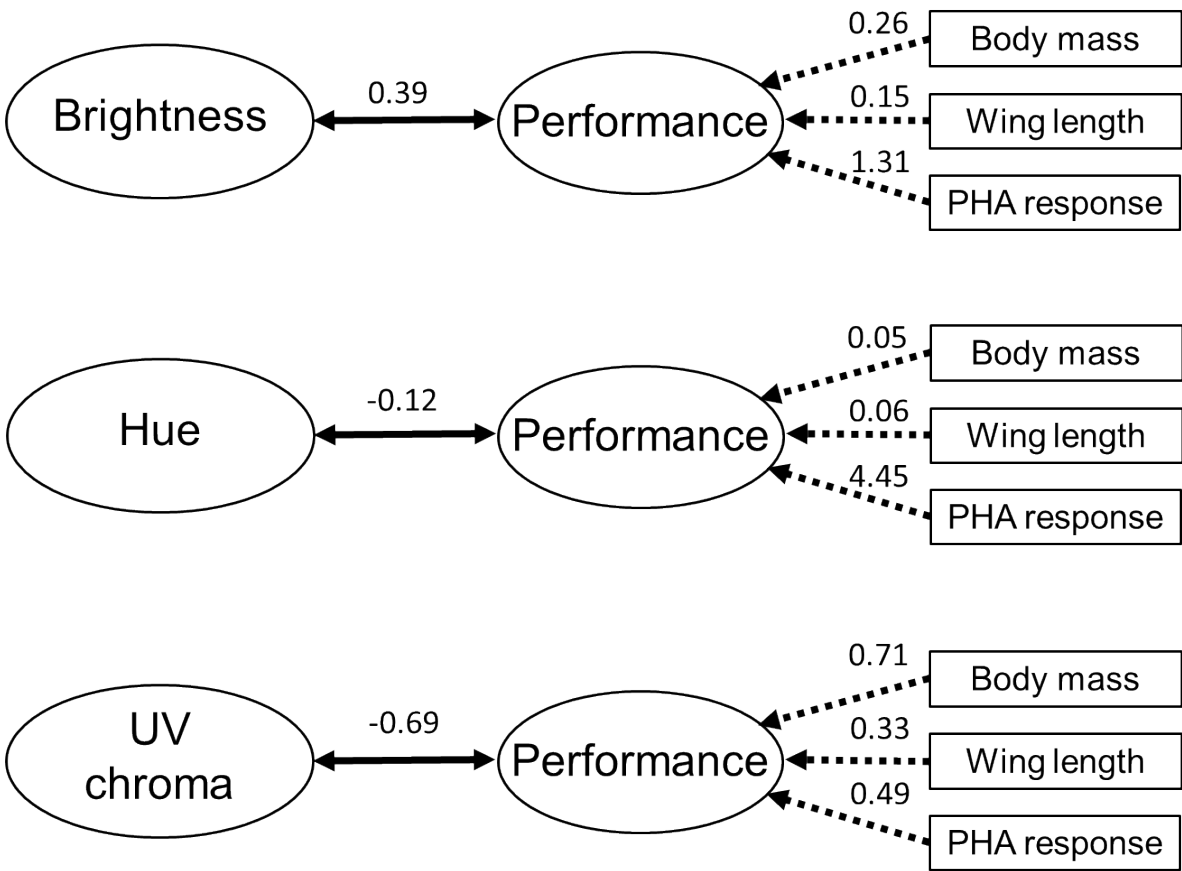
Table S22: Second residual (RES2) covariance matrix derived from the multivariate animal model. The diagonal contains RES2 variances and standard errors are printed below each estimate in grey. Covariances between color measures and performance traits are highlighted in yellow.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
Brightness	4.68 0.18					
Hue	0.82 0.55	84.91 3.39				
UV chroma	-2.98E-02 1.34E-03	-0.08 0.01	4.61E-04 1.55E-05			
PHA	8.84E-03 1.51E-02	-0.05 0.06	7.23E-05 1.26E-04	1.14E-02 1.06E-03		
Body mass	0.06 0.04	-0.50 0.18	-3.15E-04 3.30E-04	5.99E-03 3.77E-03	0.19 0.02	
Wing	0.95 0.15	-1.54 0.64	-7.07E-03 1.22E-03	7.42E-03 1.39E-02	0.33 0.05	3.35 0.24

Table S23: Phenotypic correlation matrix estimated by a multivariate mixed model. In this model, fixed effects were similar to fixed effects fitted in the multivariate animal model and only the residual component was estimated. Correlations (and their standard error) are in the lower triangle and the diagonal (underlined numbers) contains phenotypic variances (and their standard error) estimated by the model. Correlations between color measures and performance traits are highlighted in grey.

	Brightness	Hue	UV chroma	PHA	Body mass	Wing
Brightness	<u>5.85 (0.15)</u>					
Hue	-0.06 (0.02)	<u>99.5 (2.64)</u>				
UV chroma	-0.59 (0.01)	-0.36 (0.02)	<u>4.5E-04 (1.20E-05)</u>			
PHA	0.07 (0.03)	-0.05 (0.03)	-0.01 (0.03)	<u>2.55E-02 (9.18E-04)</u>		
Body mass	0.19 (0.02)	-0.06 (0.02)	-0.07 (0.02)	0.33 (0.02)	<u>0.90 (0.02)</u>	
Wing	0.32 (0.02)	-0.13 (0.02)	-0.12 (0.02)	0.21 (0.02)	0.41 (0.01)	<u>10.71 (0.27)</u>

Figure S5: Correlations (solid arrows) and loadings (dashed arrows) estimated in the structural equation models.



Text S1: R code for performing the quantitative genetic analyses

```

#Open data files
pedigree<-read.table("Pedigree_BT.txt",header=T)
Data.means<-read.table("Data_nestlings.txt",header=T)
Data.repeats<-read.table("Data_nestlings_repeats.txt",header=T)

#create the inverse of the relationship matrix from the pedigree file
library(asreml)
ainv<-asreml.Ainverse(pedigree)$ginv

#Pin function to estimate genetic correlations and their SEs based on animal model
estimates
pin<-function (object, transform)
{
  pframe <- as.list(object$gammas)
  names(pframe) <- paste("V", seq(1, length(pframe)), sep = "")
  tvalue <- eval(deriv(transform[[length(transform)]], names(pframe)), pframe)
  X <- as.vector(attr(tvalue, "gradient"))
  X[object$gammas.type == 1] <- 0
  tname <- if (length(transform) == 3)
    transform[[2]]
  else ""
  n <- length(pframe)
  i <- rep(1:n, 1:n)
  j <- sequence(1:n)
  k <- 1 + (i > j)
  Vmat <- object$ai
  se <- sqrt(sum(Vmat * X[i] * X[j] * k))
  data.frame(row.names = tname, Estimate = tvalue, SE = se)
}

#Pin function to estimate heritability and its SE based on animal model estimates
in model with heterogeneous residuals
pin2<-function (object, transform)
{
  pframe <- as.list(object$gammas)
  names(pframe) <- paste("V", seq(1, length(pframe)), sep = "")
  tvalue <- eval(deriv(transform[[length(transform)]], names(pframe)), pframe)
  X <- as.vector(attr(tvalue, "gradient"))
  # X[object$gammas.type == 1] <- 0#Do not run this line
  tname <- if (length(transform) == 3)
    transform[[2]]
  else ""
  n <- length(pframe)
  i <- rep(1:n, 1:n)
  j <- sequence(1:n)
  k <- 1 + (i > j)
  Vmat <- object$ai
  se <- sqrt(sum(Vmat * X[i] * X[j] * k))
  data.frame(row.names = tname, Estimate = tvalue, SE = se)
}

#####
#Estimate heritability of nestling color traits (using repeated measures)
#####

#Prepare data for the models
Data.repeats$Ring<-as.factor(Data.repeats$Ring)
Data.repeats$NestID<-as.factor(Data.repeats$NestID)
Data.repeats$GeneticID<-as.factor(Data.repeats$GeneticID)
Data.repeats$Year<-as.factor(Data.repeats$Year)
Data.repeats$Sex<-as.factor(Data.repeats$Sex)
Data.repeats$machine<-as.factor(Data.repeats$machine)
Data.repeats<-droplevels(Data.repeats)

```



```

#I) Brightness
modelbria<-asreml(fixed=brightness_n~ 1 + Sex +Vane + Year
                  , random= ~ped(Ring) + at(machine):ide(Ring) +at(machine):NestID
                  , rcov= ~ at(machine):units
                  , data=Data.repeats
                  ,ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit")

summary(modelbria)$varcomp
wald.asreml(modelbria,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelbria$coefficients$fixed#Coefficients of fixed effects

pin2(modelbria, h2~V3/(V1+V3+V4))#First h2
pin2(modelbria, h2~V3/(V2+V3+V5))#Second h2

pin2(modelbria, CE2~V1/(V1+V3+V4))#First VCE/VP
pin2(modelbria, CE2~V2/(V2+V3+V5))#Second VCE/VP

modelbrib<-asreml(fixed=brightness_n~ 1 + Sex +Vane + Year
                  , random= ~at(machine):ide(Ring) +at(machine):NestID
                  , rcov= ~ at(machine):units
                  , data=Data.repeats
                  ,ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit")

1-pchisq(2*(modelbria$loglik-modelbrib$loglik),1)#Test if VA in brightness is
significantly different from zero

#II) Hue
modelhuea<-asreml(fixed=hue_n~ 1 + Sex +Vane + Year
                  , random= ~ped(Ring) + at(machine):ide(Ring) +at(machine):NestID
                  , rcov= ~ at(machine):units
                  , data=Data.repeats
                  ,ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit",maxiter=100)

summary(modelhuea)$varcomp
wald.asreml(modelhuea,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelhuea$coefficients$fixed#Coefficients of fixed effects

pin2(modelhuea, h2~V3/(V1+V3+V4))#First h2
pin2(modelhuea, h2~V3/(V2+V3+V5))#Second h2

pin2(modelhuea, CE2~V1/(V1+V3+V4))#First VCE/VP
pin2(modelhuea, CE2~V2/(V2+V3+V5))#Second VCE/VP

modelhueb<-asreml(fixed=hue_n~ 1 + Sex +Vane + Year
                  , random= ~ at(machine):ide(Ring) +at(machine):NestID
                  , rcov= ~ at(machine):units
                  , data=Data.repeats
                  ,ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit")

summary(modelhueb)
1-pchisq(2*(modelhuea$loglik-modelhueb$loglik),1)#Test if VA in hue is
significantly different from zero

#III) UV chroma
modelUVa<-asreml(fixed=UV.chrome_n~ 1 + Sex +Vane + Year
                  , random= ~ped(Ring) + at(machine):ide(Ring) +at(machine):NestID
                  , rcov= ~ at(machine):units
                  , data=Data.repeats
                  ,ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit")

summary(modelUVa)$varcomp

```

```

wald.asreml(modelUVa,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelUVa$coefficients$fixed#Coefficients of fixed effects

pin2(modelUVa, h2~V3/(V1+V3+V4))#First h2
pin2(modelUVa, h2~V3/(V2+V3+V5))#Second h2

pin2(modelUVa, CE2~V1/(V1+V3+V4))#First VCE/VP
pin2(modelUVa, CE2~V2/(V2+V3+V5))#Second VCE/VP

modelUVb<-asreml(fixed=UV.chrome_n~ 1 + Sex +Vane + Year
, random= ~ at(machine):ide(Ring) +at(machine):NestID
, rcov= ~ at(machine):units
, data=Data.repeats
,ginverse=list(Ring=ainv)
, na.method.X="include", na.method.Y="omit")

1-pchisq(2*(modelUVa$loglik-modelUVb$loglik),1)#Test if VA in UV chroma is
significantly different from zero

#####
#Estimate heritability of nestling traits (using individual averages)
#####

#Prepare data for the models
Data.means$NestID<-as.factor(Data.means$NestID)
Data.means$GeneticID<-as.factor(Data.means$GeneticID)
Data.means$Year<-as.factor(Data.means$Year)
Data.means$machine<-as.factor(Data.means$machine)
Data.means$Ring<-as.factor(Data.means$Ring)
Data.means$Sex<-as.factor(Data.means$Sex)

# I) Brightness
modelbri<-asreml(fixed=brightness_n~ 1 + Sex +Vane + Year
, random= ~ped(Ring) +at(machine):NestID
, rcov= ~ at(machine):units
, data=Data.means
,ginverse=list(Ring=ainv)
, na.method.X="include", na.method.Y="omit")

summary(modelbri)$varcomp
wald.asreml(modelbri,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelbri$coefficients$fixed #Coefficients of fixed effects

pin2(modelbri, h2~V3/(V1+V3+V4))#First h2
pin2(modelbri, h2~V3/(V2+V3+V5))#Second h2

pin2(modelbri, CE~V1/(V1+V3+V4))#First VCE/VP
pin2(modelbri, CE~V2/(V2+V3+V5))#Second VCE/VP

modelbri2<-asreml(fixed=brightness_n~ 1 + Sex +Vane + Year
, random= ~at(machine):NestID
, rcov= ~ at(machine):units
, data=Data.means
, na.method.X="include", na.method.Y="omit")

summary(modelbri2)$varcomp
1-pchisq(2*(modelbri$loglik-modelbri2$loglik),1) #Test if VA in brightness is
significantly different from zero

# II) Hue
modelhue<-asreml(fixed=hue_n~ 1 +Vane+Sex+ Year
, random= ~ped(Ring) +at(machine):NestID
, rcov= ~ at(machine):units

```

```

      , data=Data.means
      , ginverse=list(Ring=ainv)
      , na.method.X="include", na.method.Y="omit")

summary(modelhue)$varcomp
wald.asreml(modelhue, ssType = "conditional", denDF="numeric") #Test significance of
fixed effects
modelhue$coefficients$fixed #Coefficients of fixed effects

pin2(modelhue, h2~V3/(V1+V3+V4)) #First h2
pin2(modelhue, h2~V3/(V2+V3+V5)) #Second h2

pin2(modelhue, CE~V1/(V1+V3+V4)) #First VCE/VP
pin2(modelhue, CE~V2/(V2+V3+V5)) #Second VCE/VP

modelhue2<-asreml(fixed=hue_n~ 1 +Vane+Sex+ Year
      , random= ~at(machine):NestID
      , rcov= ~ at(machine):units
      , data=Data.means
      , na.method.X="include", na.method.Y="omit")

summary(modelhue2)
1-pchisq(2*(modelhue$loglik-modelhue2$loglik),1) #Test if VA in hue is significantly
different from zero

# III) UV chroma

modelUV<-asreml(fixed=UV.chrome_n~ 1 +Vane +Sex + Year
      , random= ~ped(Ring) +at(machine):NestID
      , rcov= ~ at(machine):units
      , data=Data.means
      , ginverse=list(Ring=ainv)
      , na.method.X="include", na.method.Y="omit")

summary(modelUV)$varcomp

wald.asreml(modelUV, ssType = "conditional", denDF="numeric") #Test significance of
fixed effects
modelUV$coefficients$fixed #Coefficients of fixed effects

pin2(modelUV, h2~V3/(V1+V3+V4)) #First h2
pin2(modelUV, h2~V3/(V2+V3+V5)) #Second h2

pin2(modelUV, CE~V1/(V1+V3+V4)) #First VCE/VP
pin2(modelUV, CE~V2/(V2+V3+V5)) #Second VCE/VP

modelUV2<-asreml(fixed=UV.chrome_n~ 1 +Vane+Sex+ Year
      , random= ~at(machine):NestID
      , rcov= ~ at(machine):units
      , data=Data.means
      , na.method.X="include", na.method.Y="omit")

summary(modelUV2)
1-pchisq(2*(modelUV$loglik-modelUV2$loglik),1) #Test if VA in UV chroma is
significantly different from zero

# IV) PHA

modelPHA<-asreml(fixed=PHA~ 1+ Year+Sex
      , random= ~ped(Ring) +NestID
      , data=Data.means
      , ginverse=list(Ring=ainv)
      , na.method.X="include", na.method.Y="omit")

summary(modelPHA)$varcomp
wald.asreml(modelPHA, ssType = "conditional", denDF="numeric") #Test significance of
fixed effects
modelPHA$coefficients$fixed #Coefficients of fixed effects

```

```

pin(modelPHA, h2~V2/(V1+V2+V3))# h2
pin(modelPHA, CE~V1/(V1+V2+V3))# VCE/VP

modelPHA2<-asreml(fixed=PHA~ 1+ Year+Sex
                  , random= ~NestID
                  , data=Data.means
                  , na.method.X="include", na.method.Y="omit")
summary(modelPHA2)$varcomp

1-pchisq(2*(modelPHA$loglik-modelPHA2$loglik),1)#Test if VA in PHA is significantly
different from zero

# V) Size-corrected weight

modelW<-asreml(fixed=Weight_d16~ 1+ Year+Sex + Tarsus
               , random= ~ped(Ring) +NestID
               , data=Data.means
               , ginverse=list(Ring=ainv)
               , na.method.X="include", na.method.Y="omit")

summary(modelW)$varcomp
wald.asreml(modelW,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelW$coefficients$fixed#Coefficients of fixed effects

pin(modelW, h2~V2/(V1+V2+V3))# h2
pin(modelW, CE~V1/(V1+V2+V3))# VCE/VP

modelW2<-asreml(fixed=Weight_d16~ 1+ Year+Sex + Tarsus
                , random= ~NestID
                , data=Data.means
                , na.method.X="include", na.method.Y="omit")

summary(modelW2)$varcomp
1-pchisq(2*(modelW$loglik-modelW2$loglik),1)#Test if VA in weight is significantly
different from zero

# VI) Wing length
modelWing<-asreml(fixed=Wing~ 1+ Year+Sex
                  , random= ~ped(Ring) +NestID
                  , data=Data.means
                  , ginverse=list(Ring=ainv)
                  , na.method.X="include", na.method.Y="omit")

summary(modelWing)$varcomp
wald.asreml(modelWing,ssType = "conditional", denDF="numeric")#Test significance of
fixed effects
modelWing$coefficients$fixed#Coefficients of fixed effects

pin(modelWing, h2~V2/(V1+V2+V3))# h2
pin(modelWing, CE~V1/(V1+V2+V3))# VCE/VP

modelWing2<-asreml(fixed=Wing~ 1+ Year+Sex
                   , random= ~NestID
                   , data=Data.means
                   , na.method.X="include", na.method.Y="omit")

summary(modelWing2)$varcomp
1-pchisq(2*(modelWing$loglik-modelWing2$loglik),1)#Test if VA in Wing length is
significantly different from zero

#####
#Multivariate models
#####

###Multivariate model for all condition traits

```

```

multi.nestling.w<-asreml(cbind(PHA,Weight_d16,Wing)~ trait + trait:Year + trait:Sex
+ at(trait,2):Tarsus,

random=~us(trait,init=c(0.005,0.009,0.3,0.03,0.3,9)):ped(Ring)+
us(trait,init=c(0.007,0.3,0.47,0.08,0.9,3.6)):NestID,
      rcov=~units:diag(trait,init=c(0.01, 0.16, 0.7)),
      ginverse=list(Ring=ainv),
      data = Data.means,na.method.X="include",
      maxiter=100)
summary(multi.nestling.w)
pin(multi.nestling.w, cor~V8/(sqrt(V7*V9)):#Weight-PHA
pin(multi.nestling.w, cor~V10/(sqrt(V7*V12)):#Wing-PHA
pin(multi.nestling.w, cor~V11/(sqrt(V12*V9)):#Weight-Wing

#Check if the correlations between performance traits are influenced by wing
thickness before injection
multi.nestling.w2<-asreml(cbind(PHA,Weight_d16,Wing,WingWeb_d13)~ trait +
trait:Year + trait:Sex + at(trait,2):Tarsus,
      random=~us(trait,init=c(0.006,0.02,0.37,0.06,0.86,5.27,-
0.03,0.1,0.1,0.57)):ped(Ring)+
us(trait,init=c(0.007,0.03,0.48,0.06,0.73,4.64,0.03,0.1,0.1,3.97)):NestID,
      rcov=~units:diag(trait,init=c(0.01,0.12,2.28,4.19)),
      ginverse=list(Ring=ainv),
      data = Data.means,na.method.X="include",
      maxiter=300)
summary(multi.nestling.w2)
pin(multi.nestling.w2, cor~V12/(sqrt(V11*V13))
pin(multi.nestling.w2, cor~V14/(sqrt(V11*V16))
pin(multi.nestling.w2, cor~V15/(sqrt(V13*V16))

#Test these correlations 1 by 1
sv<-asreml(cbind(PHA,Weight_d16,Wing)~ trait + trait:Year + trait:Sex +
at(trait,2):Tarsus,
      random=~us(trait):ped(Ring)+
us(trait,init=c(0.007,0.3,0.47,0.08,0.9,3.6)):NestID,
      rcov=~units:diag(trait,init=c(0.01, 0.16, 0.7)),
      ginverse=list(Ring=ainv),
      data = Data.means,na.method.X="include",
      maxiter=100,start.values = T)
gam<-sv$gammas.table
gam$Value[5]<-0#Values 2,4,5
gam$Constraint[5]<-"F"

multi.nestling.wb<-asreml(cbind(PHA,Weight_d16,Wing)~ trait + trait:Year +
trait:Sex + at(trait,2):Tarsus,
      random=~us(trait):ped(Ring)+
us(trait,init=c(0.007,0.3,0.47,0.08,0.9,3.6)):NestID,
      rcov=~units:diag(trait,init=c(0.01, 0.16, 0.7)),
      ginverse=list(Ring=ainv),
      data = Data.means,na.method.X="include",
      maxiter=100,G.param = gam)
summary(multi.nestling.wb)

1-pchisq(2*(multi.nestling.w$loglik-multi.nestling.wb$loglik),1)#Test for the
statistical significance of the genetic correlation

###Multivariate model for all coloration traits

multi.nestling.c<-asreml(cbind(brightness_n,UV.chrome_n,hue_n)~ trait + trait:Year
+ trait:Sex + trait:Vane,
      random=~ us(trait,init=c(0.90,-1.22e-3,1.62e-5,-0.25,-6e-
3,13.11)):at(machine,init=c(1,2)):NestID + us(trait,init=c(0.24,-5e-4,8e-6,-0.4,-
4e-3,8)):ped(Ring),
      rcov=~ units:us(trait,init=c(2,-1.44e-3,3.7e-5,-0.56,-5.8e-
3,40.5)):at(machine,init=c(1,2)),
      ginverse=list(Ring=ainv),
      data = Data.means,na.method.X="include",

```

```

maxiter=300)
summary(multi.nestling.c)$varcomp

#Test these correlations 1 by 1
sv<-asreml(cbind(brightness_n,UV.chrome_n,hue_n)~ trait + trait:Year + trait:Sex +
trait:Vane,
  random=~ us(trait,init=c(0.90,-1.22e-3,1.62e-5,-0.25,-6e-
3,13.11)):at(machine,init=c(1,2)):NestID + us(trait,init=c(0.24,-5e-4,8e-6,-0.4,-
4e-3,8)):ped(Ring),
  rcov=~ units:us(trait,init=c(2,-1.44e-3,3.7e-5,-0.56,-5.8e-
3,40.5)):at(machine,init=c(1,2)),
  ginverse=list(Ring=ainv),
  data = Data.means,na.method.X="include",
  maxiter=300,start.values = T)

gam<-sv$gammas.table
gam$Value[17]<-0#values 14,16,17
gam$Constraint[17]<-"F"

multi.nestling.cb<-asreml(cbind(brightness_n,UV.chrome_n,hue_n)~ trait + trait:Year
+ trait:Sex + trait:Vane,
  random=~ us(trait,init=c(0.90,-1.22e-3,1.62e-5,-0.25,-6e-
3,13.11)):at(machine,init=c(1,2)):NestID + us(trait):ped(Ring),
  rcov=~ units:us(trait,init=c(2,-1.44e-3,3.7e-5,-0.56,-5.8e-
3,40.5)):at(machine,init=c(1,2)),
  ginverse=list(Ring=ainv),
  data = Data.means,na.method.X="include",
  maxiter=300,G.param=gam)

summary(multi.nestling.cb)
1-pchisq(2*(multi.nestling.c$loglik-multi.nestling.cb$loglik),1)#Test for the
statistical significance of the genetic correlation

###Multivariate model for all six traits

#Need to specify starting values
sv<-asreml(cbind(brightness_n,hue_n,UV.chrome_n,PHA, Weight_d16,Wing)~ trait +
trait:Year + trait:Sex + at(trait,1):Vane+ at(trait,2):Vane+ at(trait,3):Vane+
at(trait,5):Tarsus,
  random=~ us(trait):ped(Ring) + us(trait):at(machine):NestID ,
  rcov=~ units:us(trait):at(machine),
  ginverse=list(Ring=ainv),
  data = Data.means,na.method.X="include",
  maxiter=300,start.values = TRUE)
gam<-sv$gammas.table

gam[1:21,1:2]#pedigree
gam$Value[1:21]<-c(2.77E-01, -7.98E-01, 4.45E+00, -1.60E-04, -1.63E-03,
5.19E-06, -1.85E-03,
-5.69E-03, -8.29E-05, 5.32E-03, 5.31E-02, 1.28E-01,
-1.86E-04, 8.15E-03,
2.30E-01, 3.44E-01, -1.42E+00, -1.01E-03, 3.04E-02,
1.65E-01, 1.73E+00)

gam[22:42,1:2]#NestID1
gam$Value[c(22:42)]<-c(1.04E+00, -4.21E-01, 1.29E+01, -1.50E-03, -4.17E-03,
1.74E-05,4.19E-02,
-9.47E-03, 7.64E-05, 1.12E-02, 3.40E-01, 3.06E-01,
9.01E-04,5.25E-02,
5.96E-01, 1.50E+00, 1.21E+00, 1.80E-04, 1.41E-01,
1.18E+00, 7.92E+00)

gam[43:63,1:2]#NestID2
gam$Value[c(43:63)]<-c(1.95E+00, -1.52E+00, 2.51E+01, -1.16E-02, -1.74E-02,
1.44E-04, 1.35E-02,
3.47E-03, -1.01E-04, 3.45E-03, 3.22E-01, -8.74E-02,
-2.20E-03, 1.89E-02,

```

```

        4.61E-01, 1.51E+00, -2.00E+00, -7.99E-03, 3.69E-03,
        6.67E-01, 4.18E+00)

gam[65:85,1:2]#residual1
gam$Value[c(65:85)]<-c(2.02E+00, -1.70E-02, 4.53E+01, -1.75E-03, -1.01E-02,
        4.08E-05, -3.98E-03,
        2.56E-02, 1.02E-04, 1.44E-02, 1.11E-02, -1.93E-01,
        6.53E-04, 1.51E-02,
        2.73E-01, 4.08E-01, 1.53E+00, 3.81E-03, 4.60E-02,
        7.21E-01, 7.77E+00)
gam[87:107,1:2]#residual2
gam$Value[c(87:107)]<-c(4.68E+00, 8.19E-01, 8.49E+01, -2.98E-02, -8.10E-02
        ,4.61E-04 ,8.83E-03,
        -5.42E-02, 7.22E-05, 1.14E-02, 5.60E-02, -
        5.04E-01, -3.15E-04, 5.99E-03,
        1.88E-01, 9.52E-01, -1.54E+00, -7.07E-03, 7.48E-03,
        3.31E-01, 3.34E+00)

#Run the model
multi.total.nestling<-asreml(cbind(brightness_n,hue_n,UV.chrome_n,PHA,
Weight_d16,Wing)~ trait + trait:Year + trait:Sex + at(trait,1):Vane+
at(trait,2):Vane+ at(trait,3):Vane+ at(trait,5):Tarsus,
        random=~ us(trait):ped(Ring) +
us(trait):at(machine):NestID ,
        rcov=~ units:us(trait):at(machine),
        ginverse=list(Ring=ainv),
        data = Data.means,na.method.X="include",G.param=gam,
R.param=gam,
        maxiter=100)

summary(multi.total.nestling)$varcomp

#Calculate genetic correlations and their SE using the pin function

pin(multi.total.nestling,rg~ V44/sqrt(V43*V45))#hue-bri
pin(multi.total.nestling,rg~ V46/sqrt(V43*V48))#UV-bri
pin(multi.total.nestling,rg~ V47/sqrt(V45*V48))#UV-hue

pin(multi.total.nestling,rg~ V49/sqrt(V43*V52))#PHA-bri
pin(multi.total.nestling,rg~ V50/sqrt(V45*V52))#PHA-hue
pin(multi.total.nestling,rg~ V51/sqrt(V48*V52))#PHA-UV

pin(multi.total.nestling,rg~ V53/sqrt(V43*V57))#Weight- Bri
pin(multi.total.nestling,rg~ V54/sqrt(V45*V57))#Weight- Hue
pin(multi.total.nestling,rg~ V55/sqrt(V48*V57))#Weight- UV
pin(multi.total.nestling,rg~ V56/sqrt(V57*V52))#Weight- PHA

pin(multi.total.nestling,rg~ V58/sqrt(V43*V63))#Wing -Bri
pin(multi.total.nestling,rg~ V59/sqrt(V45*V63))#Wing -Hue
pin(multi.total.nestling,rg~ V60/sqrt(V48*V63))#Wing- UV
pin(multi.total.nestling,rg~ V61/sqrt(V52*V63))#Wing -PHA
pin(multi.total.nestling,rg~ V62/sqrt(V57*V63))#Wing -Weight

###Multivariate model on the phenotypic level

multi.pheno.nestling<-asreml(cbind(brightness_n,hue_n,UV.chrome_n,PHA,
Weight_d16,Wing)~ trait + trait:Year + trait:Sex + at(trait,1):Vane+
at(trait,2):Vane+ at(trait,3):Vane+ at(trait,5):Tarsus,
        rcov=~ units:us(trait),
        data = Data.means,na.method.X="include",maxiter=100)
summary(multi.pheno.nestling)$varcomp

#Calculate phenotypic correlations and their SE using the pin function

pin(multi.pheno.nestling,rg~ V3/sqrt(V2*V4))#hue-bri
pin(multi.pheno.nestling,rg~ V5/sqrt(V2*V7))#UV-bri
pin(multi.pheno.nestling,rg~ V6/sqrt(V4*V7))#UV-hue

```

```

pin(multi.pheno.nestling,rg~ V8/sqrt(V2*V11))#PHA-bri
pin(multi.pheno.nestling,rg~ V9/sqrt(V4*V11))#PHA-hue
pin(multi.pheno.nestling,rg~ V10/sqrt(V7*V11))#PHA-UV

pin(multi.pheno.nestling,rg~ V12/sqrt(V2*V16))#Weight- Bri
pin(multi.pheno.nestling,rg~ V13/sqrt(V4*V16))#Weight- Hue
pin(multi.pheno.nestling,rg~ V14/sqrt(V7*V16))#Weight- UV
pin(multi.pheno.nestling,rg~ V15/sqrt(V11*V16))#Weight- PHA

pin(multi.pheno.nestling,rg~ V17/sqrt(V2*V22))#Wing -Bri
pin(multi.pheno.nestling,rg~ V18/sqrt(V4*V22))#Wing -Hue
pin(multi.pheno.nestling,rg~ V19/sqrt(V7*V22))#Wing- UV
pin(multi.pheno.nestling,rg~ V20/sqrt(V11*V22))#Wing -PHA
pin(multi.pheno.nestling,rg~ V21/sqrt(V16*V22))#Wing -Weight

#####
#A different approach to calculate heritability of PHA
#Excludes measurement error
#####
WingWebs<-read.table("WingWebs.txt",header=T)
WingWebs$Ring<-as.factor(WingWebs$Ring)
WingWebs$NestID<-as.factor(WingWebs$NestID)
WingWebs$Year<-as.factor(WingWebs$Year)
WingWebs$Sex<-as.factor(WingWebs$Sex)

#Run a multivariate model with repeated measures of wing web before and after
injection
multi<-asreml(cbind(WingWeb_d13,WingWeb_d14)~ trait + trait:Year + trait:Sex ,
              random=~us(trait):ped(Ring)+ + us(trait):ide(Ring)+us(trait):NestID,
              rcov=~units:diag(trait),
              ginverse=list(Ring=ainv),
              data = WingWebs,na.method.X="include",
              maxiter=1000)
summary(multi)$varcomp

#Calculate heritability of the difference=PHA
pin(multi, h2~(V4+V6-2*V5) / ((V4+V6-2*V5)+(V1+V3-2*V2)+(V7+V9-2*V8)))#heritability
pin(multi, CE2~(V1+V3-2*V2) / ((V4+V6-2*V5)+(V1+V3-2*V2)+(V7+V9-2*V8)))#VCE/VP

#####
#Estimate cross-sex genetic correlations
#####

#Create the table for analyses
Data.means.fem<-Data.means[Data.means$Sex=="f",]
Data.means.mal<-Data.means[Data.means$Sex=="m",]

names(Data.means.fem)[5:10]<-paste(names(Data.means.fem)[5:10],"_f",sep="")
names(Data.means.mal)[5:10]<-paste(names(Data.means.mal)[5:10],"_m",sep="")

Data.means.mal$hue_n_f<-NA
Data.means.mal$brightness_n_f<-NA
Data.means.mal$UV.chrome_n_f<-NA
Data.means.mal$PHA_f<-NA
Data.means.mal$Weight_d16_f<-NA
Data.means.mal$Wing_f<-NA

Data.means.fem$hue_n_m<-NA
Data.means.fem$brightness_n_m<-NA
Data.means.fem$UV.chrome_n_m<-NA
Data.means.fem$PHA_m<-NA
Data.means.fem$Weight_d16_m<-NA
Data.means.fem$Wing_m<-NA

Data.means.fem<-Data.means.fem[,names(Data.means.mal)]
names(Data.means.fem)

```



```

Data.means.sexes<-rbind(Data.means.mal,Data.means.fem)
Data.means.sexes<-Data.means.sexes[order(Data.means.sexes$machine),]

#Run the bivariate model for each trait
biv.sexes.bri<-asreml(cbind(brightness_n_m,brightness_n_f)~ trait + trait:Year +
trait:Vane,
                      random=~us(trait):ped(Ring)+ us(trait):NestID:at(machine)
,
                      rcov=~units:diag(trait):at(machine),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=500)
summary(biv.sexes.bri)
pin(biv.sexes.bri, cor~V8/(sqrt(V7*V9)))#r=0.99 se=0.53

biv.sexes.hue<-asreml(cbind(hue_n_m,hue_n_f)~ trait + trait:Year + trait:Vane,
                      random=~us(trait):ped(Ring)+ us(trait):NestID:at(machine) ,
                      rcov=~units:diag(trait):at(machine),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=500)
summary(biv.sexes.hue)
pin(biv.sexes.hue, cor~V8/(sqrt(V7*V9)))#r=0.59 se=0.48

biv.sexes.UV<-asreml(cbind(UV.chrome_n_f,UV.chrome_n_m)~ trait + trait:Year +
trait:Vane,
                      random=~us(trait):ped(Ring)+ us(trait):NestID:at(machine) ,
                      rcov=~units:diag(trait):at(machine),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=500)
biv.sexes.UV<-update(biv.sexes.UV)
summary(biv.sexes.UV)

pin(biv.sexes.UV, cor~V8/(sqrt(V7*V9)))#r=0.95 se=0.52

biv.sexes.PHA<-asreml(cbind(PHA_f,PHA_m)~ trait + trait:Year,
                      random=~us(trait):ped(Ring)+ us(trait):NestID ,
                      rcov=~units:diag(trait),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=400)
summary(biv.sexes.PHA)

pin(biv.sexes.PHA, cor~V5/(sqrt(V4*V6)))#r=0.98 se=0.17

biv.sexes.W<-asreml(cbind(Weight_d16_f,Weight_d16_m)~ trait + trait:Year +
trait:Tarsus,
                      random=~us(trait):ped(Ring)+ us(trait):NestID ,
                      rcov=~units:diag(trait),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=300)
summary(biv.sexes.W)

pin(biv.sexes.W, cor~V5/(sqrt(V4*V6)))#r=0.92 se=0.05

biv.sexes.Wing<-asreml(cbind(Wing_f,Wing_m)~ trait + trait:Year,
                      random=~us(trait):ped(Ring)+ us(trait):NestID ,
                      rcov=~units:diag(trait),
                      ginverse=list(Ring=ainv),
                      data = Data.means.sexes,na.method.X="include",
                      maxiter=300)
summary(biv.sexes.Wing)

pin(biv.sexes.Wing, cor~V5/(sqrt(V4*V6)))#r=0.94 se=0.08

```

Text S2: R code for performing structural equation modelling on the G matrix

```

library(lavaan)

#Extract additive genetic (co)variances estimates from the full model
Gmat<-summary(multi.total.nestling)$varcomp[43:63,]

#Create covariance matrix based on these estimates
cov.color_n_gen <- matrix(Gmat[c(1,2,4,7,11,16,
                                2,3,5,8,12,17,
                                4,5,6,9,13,18,
                                7,8,9,10,14,19,
                                11,12,13,14,15,20,
                                16,17,18,19,20,21),1],6,6,byrow=TRUE)

rownames(cov.color_n_gen) <- colnames(cov.color_n_gen) <- c("BriN","Hue","UV",
"PHA","Weight","Wing")

#Transform it into a correlation martix
cor.color_n_gen <- cov2cor(cov.color_n_gen)

#Model where the three performance traits load on a single "performance" factor
HS.modelW <-
  'L1 =~lam1*Weight+ lam2*Wing + lam3*PHA
Weight~~b1*Weight
Wing~~b2*Wing
PHA~~b3*PHA
b1==1-(lam1^2)
b2==1-(lam2^2)
b3==1-(lam3^2)
'

fitW <- cfa(HS.modelW, sample.cov =cor.color_n_gen,sample.nobs=306,std.lv=TRUE)
standardizedsolution(fitW)

#First model: estimate the correlation between brightness and performance
HS.modelA <-
  'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
L2=~1*BriN
PHA~~b1*PHA
Weight~~b2*Weight
Wing~~b3*Wing
BriN~~0*BriN
b1==1-(lam1^2)
b2==1-(lam2^2)
b3==1-(lam3^2) '
fitA <- cfa(HS.modelA, sample.cov =cor.color_n_gen,sample.nobs=306,std.lv=TRUE)
standardizedsolution(fitA)

#Second model: estimate the correlation between hue and performance

HS.modelB <-
  'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
L2=~1*Hue
PHA~~b1*PHA
Weight~~b2*Weight
Wing~~b3*Wing
Hue~~0*Hue
b1==1-(lam1^2)
b2==1-(lam2^2)
b3==1-(lam3^2) '
fitB <- sem(HS.modelB, sample.cov =cor.color_n_gen,sample.nobs=306,std.lv=TRUE)
standardizedsolution(fitB)

#Third model: estimate the correlation between UV chroma and performance
HS.modelC <-

```

```
'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
L2=~1*UV
PHA~~b1*PHA
Weight~~b2*Weight
Wing~~b3*Wing
UV~~0*UV
b1==1-(lam1^2)
b2==1-(lam2^2)
b3==1-(lam3^2) '
fitC <- cfa(HS.modelC, sample.cov =cor.color_n_gen,sample.nobs=306,std.lv=TRUE)
standardizedsolution(fitC)
```

Text S3: R code for performing simulations

```

library(lavaan)
library(asreml)
library(pedantics)
#Open data files
pedigree<-read.table("Pedigree_BT.txt",header=T)
ainv<-asreml.Ainverse(pedigree)$ginv

data.chicks<-read.table("Data_nestlings.txt",header=T)
data.chicks<-unique(data.chicks[,c(1,3)])
NestIDS<-unique(data.chicks$NestID)
names(data.chicks)[1]<-"id"
#Extract additive genetic (co)variances estimates from the full model
Gmat<-summary(multi.total.nestling)$varcomp[43:63,1]
Emat1<-summary(multi.total.nestling)$varcomp[65:85,1]
CEmat1<-summary(multi.total.nestling)$varcomp[1:21,1]

#Create covariance matrices based on these estimates
SigmaG <- matrix(Gmat[c(1,2,4,7,11,16,
                        2,3,5,8,12,17,
                        4,5,6,9,13,18,
                        7,8,9,10,14,19,
                        11,12,13,14,15,20,
                        16,17,18,19,20,21)],6,6,byrow=TRUE)

SigmaE <- matrix(Emat1[c(1,2,4,7,11,16,
                        2,3,5,8,12,17,
                        4,5,6,9,13,18,
                        7,8,9,10,14,19,
                        11,12,13,14,15,20,
                        16,17,18,19,20,21)],6,6,byrow=TRUE)

SigmaCE <- matrix(CEmat1[c(1,2,4,7,11,16,
                        2,3,5,8,12,17,
                        4,5,6,9,13,18,
                        7,8,9,10,14,19,
                        11,12,13,14,15,20,
                        16,17,18,19,20,21)],6,6,byrow=TRUE)

#Run simulations
Results.sim<-data.frame("iteration"=NA,
"Conv1"=NA,"Conv2"=NA,"Conv3"=NA,"Bri.Perf"=NA, "Hue.Perf"=NA, "UV.Perf"=NA,
                        "lam1a"=NA, "lam2a"=NA,"lam3a"=NA,"lam1b"=NA,
"lam2b"=NA,"lam3b"=NA,"lam1c"=NA, "lam2c"=NA,"lam3c"=NA)

for ( i in 1:1000){

  Results.sim[i,1]<-i
  #Simulate data using pedantics
  simPhen<-phensim(pedigree,traits=6, randomA=SigmaG,randomE=SigmaE)$phenotypes

  #Add CE effects
  simPhen$id<-as.factor(simPhen$id)
  CEEffects<-as.data.frame(rmvnorm(length(NestIDS),sigma=SigmaCE))
  CEEffects$NestID<-as.factor(NestIDS)
  simPhen<-merge(simPhen,data.chicks)
  simPhen<-merge(simPhen,CEEffects)
  Datasim<-simPhen[,c(1,2)]
  Datasim$trait_1<-simPhen$trait_1+simPhen$V1
  Datasim$trait_2<-simPhen$trait_2+simPhen$V2
  Datasim$trait_3<-simPhen$trait_3+simPhen$V3
  Datasim$trait_4<-simPhen$trait_4+simPhen$V4
  Datasim$trait_5<-simPhen$trait_5+simPhen$V5
  Datasim$trait_6<-simPhen$trait_6+simPhen$V6
  Datasim$NestID<-as.factor(Datasim$NestID)
  ###Analyse using asreml

```

```

#Run the models: need to run 3 different models because 6-trait model never
converges despite starting values
sv1<-
c(SigmaG[1,1],SigmaG[1,4],SigmaG[4,4],SigmaG[1,5],SigmaG[4,5],SigmaG[5,5],SigmaG[1,
6],SigmaG[4,6],SigmaG[5,6],SigmaG[6,6])
sv2<-
c(SigmaG[2,2],SigmaG[2,4],SigmaG[4,4],SigmaG[2,5],SigmaG[4,5],SigmaG[5,5],SigmaG[2,
6],SigmaG[4,6],SigmaG[5,6],SigmaG[6,6])
sv3<-
c(SigmaG[3,3],SigmaG[3,4],SigmaG[4,4],SigmaG[3,5],SigmaG[4,5],SigmaG[5,5],SigmaG[3,
6],SigmaG[4,6],SigmaG[5,6],SigmaG[6,6])

sv1b<-
c(SigmaE[1,1],SigmaE[1,4],SigmaE[4,4],SigmaE[1,5],SigmaE[4,5],SigmaE[5,5],SigmaE[1,
6],SigmaE[4,6],SigmaE[5,6],SigmaE[6,6])
sv2b<-
c(SigmaE[2,2],SigmaE[2,4],SigmaE[4,4],SigmaE[2,5],SigmaE[4,5],SigmaE[5,5],SigmaE[2,
6],SigmaE[4,6],SigmaE[5,6],SigmaE[6,6])
sv3b<-
c(SigmaE[3,3],SigmaE[3,4],SigmaE[4,4],SigmaE[3,5],SigmaE[4,5],SigmaE[5,5],SigmaE[3,
6],SigmaE[4,6],SigmaE[5,6],SigmaE[6,6])

sv1c<-
c(SigmaCE[1,1],SigmaCE[1,4],SigmaCE[4,4],SigmaCE[1,5],SigmaCE[4,5],SigmaCE[5,5],Sig
maCE[1,6],SigmaCE[4,6],SigmaCE[5,6],SigmaCE[6,6])
sv2c<-
c(SigmaCE[2,2],SigmaCE[2,4],SigmaCE[4,4],SigmaCE[2,5],SigmaCE[4,5],SigmaCE[5,5],Sig
maCE[2,6],SigmaCE[4,6],SigmaCE[5,6],SigmaCE[6,6])
sv3c<-
c(SigmaCE[3,3],SigmaCE[3,4],SigmaCE[4,4],SigmaCE[3,5],SigmaCE[4,5],SigmaCE[5,5],Sig
maCE[3,6],SigmaCE[4,6],SigmaCE[5,6],SigmaCE[6,6])

Test.multi1<-asreml(cbind(trait_1,trait_4, trait_5,trait_6)~ trait,
                    random=~ us(trait,init=sv1):ped(id)+ us(trait,init=sv1c):NestID
,
                    rcov=~ units:us(trait,init=sv1b),
                    ginverse=list(id=ainv),
                    data = Datasim,na.method.X="include",
                    maxiter=300)

Test.multi2<-asreml(cbind(trait_2,trait_4, trait_5,trait_6)~ trait,
                    random=~ us(trait,init=sv2):ped(id)+ us(trait,init=sv2c):NestID
,
                    rcov=~ units:us(trait,init=sv2b),
                    ginverse=list(id=ainv),
                    data = Datasim,na.method.X="include",
                    maxiter=300)

Test.multi3<-asreml(cbind(trait_3,trait_4, trait_5,trait_6)~ trait,
                    random=~ us(trait,init=sv3):ped(id)+ us(trait,init=sv3c):NestID
,
                    rcov=~ units:us(trait,init=sv3b),
                    ginverse=list(id=ainv),
                    data = Datasim,na.method.X="include",
                    maxiter=300)

Results.sim[i,2]<-Test.multi1$converge
Results.sim[i,3]<-Test.multi2$converge
Results.sim[i,4]<-Test.multi3$converge

GmatSim1<-summary(Test.multi1)$varcomp[11:20,1]
GmatSim2<-summary(Test.multi2)$varcomp[11:20,1]
GmatSim3<-summary(Test.multi3)$varcomp[11:20,1]

#Extract covariance matrix
cov1<- matrix(GmatSim1[c(1,2,4,7,

```

```

      2,3,5,8,
      4,5,6,9,
      7,8,9,10)],4,4,byrow=TRUE)

rownames(cov1) <- colnames(cov1) <- c("BriN","PHA","Weight","Wing")

cov2<- matrix(Gmatsim2[c(1,2,4,7,
      2,3,5,8,
      4,5,6,9,
      7,8,9,10)],4,4,byrow=TRUE)

rownames(cov2) <- colnames(cov2) <- c("Hue","PHA","Weight","Wing")

cov3<- matrix(Gmatsim3[c(1,2,4,7,
      2,3,5,8,
      4,5,6,9,
      7,8,9,10)],4,4,byrow=TRUE)

rownames(cov3) <- colnames(cov3) <- c("UV","PHA","Weight","Wing")

#Transform it into a correlation martix
cor1 <- cov2cor(cov1)
cor2 <- cov2cor(cov2)
cor3 <- cov2cor(cov3)

###Run SEMS on this correlation matrix
#Test Brightness and performance
HS.modelA <-
  'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
  L2=~1*BriN
  PHA~~b1*PHA
  Weight~~b2*Weight
  Wing~~b3*Wing
  BriN~~0*BriN
  b1==1-(lam1^2)
  b2==1-(lam2^2)
  b3==1-(lam3^2) '

fitA <- cfa(HS.modelA, sample.cov =cor1,sample.nobs=306,std.lv=TRUE)
solA<-data.frame(standardizedsolution(fitA))
Results.sim[i,"Bri.Perf"]<-solA[11,4]

#Test Hue and performance
HS.modelB <-
  'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
  L2=~1*Hue
  PHA~~b1*PHA
  Weight~~b2*Weight
  Wing~~b3*Wing
  Hue~~0*Hue
  b1==1-(lam1^2)
  b2==1-(lam2^2)
  b3==1-(lam3^2) '

fitB <- sem(HS.modelB, sample.cov =cor2,sample.nobs=306,std.lv=TRUE)
solB<-data.frame(standardizedsolution(fitB))
Results.sim[i,"Hue.Perf"]<-solB[11,4]

#Test UV and performance
HS.modelC <-
  'L1 =~lam1*PHA +lam2*Weight+ lam3*Wing
  L2=~1*UV
  PHA~~b1*PHA
  Weight~~b2*Weight
  Wing~~b3*Wing
  UV~~0*UV
  b1==1-(lam1^2)

```

```

b2==1-(lam2^2)
b3==1-(lam3^2) '

fitC <- cfa(HS.modelC, sample.cov =cor3,sample.nobs=306,std.lv=TRUE)
solC<-data.frame(standardizedsolution(fitC))
Results.sim[i,"UV.Perf"]<-solC[11,4]

Results.sim[i,"lam1a"]<-solA[1,4]
Results.sim[i,"lam2a"]<-solA[2,4]
Results.sim[i,"lam3a"]<-solA[3,4]

Results.sim[i,"lam1b"]<-solB[1,4]
Results.sim[i,"lam2b"]<-solB[2,4]
Results.sim[i,"lam3b"]<-solB[3,4]

Results.sim[i,"lam1c"]<-solC[1,4]
Results.sim[i,"lam2c"]<-solC[2,4]
Results.sim[i,"lam3c"]<-solC[3,4]

}###End of simulations

#Save results
write.table(Results.sim,"Result.sim.txt",row.names = F)

#Open results
Results.sim<-read.table("Result.sim.txt",header=T)

#Keep only the models where the 3 performance traits correlate positively
reduced1<-Results.sim[Results.sim$lam1a>0.05
&Results.sim$lam2a>0.05&Results.sim$lam3a>0.05&Results.sim$Conv1==TRUE,c(1,5,8:10)
]
reduced2<-Results.sim[Results.sim$lam1b>0.05
&Results.sim$lam2b>0.05&Results.sim$lam3b>0.05&Results.sim$Conv2==TRUE,c(1,6,11:13)
]
reduced3<-Results.sim[Results.sim$lam1c>0.05
&Results.sim$lam2c>0.05&Results.sim$lam3c>0.05&Results.sim$Conv3==TRUE,
c(1,7,14:16)]

hist(reduced1$Bri.Perf,xlim=c(-1,1),breaks=20)
hist(reduced2$Hue.Perf,xlim=c(-2,1),breaks=20)
hist(reduced3$UV.Perf,xlim=c(-2,1),breaks=20)

#Median and 95% CI of correlation estimates
median(reduced1$Bri.Perf)
median(reduced2$Hue.Perf)
median(reduced3$UV.Perf)

quantile(reduced1$Bri.Perf,probs=c(0.025,0.975))
quantile(reduced2$Hue.Perf,probs=c(0.025,0.975))
quantile(reduced3$UV.Perf,probs=c(0.025,0.975))

```

Dear Editor of Journal of Evolutionary Biology,

Thank you for your quick reply. We made the corrections that you requested in our manuscript "Tail color signals performance in blue tit nestlings" (JEB-2018-00555.R3).

Sincerely,

The author

JEB ms # JEB-2018-00555.R2

Dear Dr. Class,

I am willing to consider acceptance of your paper for publication in JEB, provided you revise it along the lines recommended.

- Remove double brackets $)),)$, $(($ throughout (e.g. l 244)
- state what you're reporting (line 250 - what's in the brackets? Report consistently - if that's se, then it's inconsistently reported - see line 256).
- report 95%CI as range (with a dash between, not a comma), throughout
- use space consistently in reporting results throughout (before and after numbers, =, 95%CI, 95 % CI ect.)

Please pay careful attention to the formatting of tables, figures and references, as well as the style used for reporting the results of statistical tests (see Instructions for Authors, <http://onlinelibrary.wiley.com/journal/10.1111/%28ISSN%291420-9101/homepage/ForAuthors.html>)

Please make sure any in-line statistics conform to the Instructions for authors ("In-line statistical results should be presented as Test-statistics: degrees of freedom as subscript(s) to test-statistics (e.g. $F_{1,12} = \dots$ or $t_8 = \dots$), followed by P-value., e.g. ($F_{1,12} = 4.931$, $P = 0.0464$). Statistical results in tables should be comprehensive, allowing future meta-analyses. Depending on the details of the analyses, results reported may include parameter estimates, test-statistics, degrees of freedom, significance levels and err/residual model information (e.g. error MS's and df's in ANOVA or regression models). Since exact P-values can be useful for meta-analyses, we recommend that these are quoted even when non-significant, e.g. $t_{23}=0.25$, $P=0.34$, or $F_{2,32}=1.12$, $P=0.55$. However, non significant tests (i.e. $P > 0.05$) should always be interpreted as such.")

Please submit your revised paper in an editable format, within 30 days from the date of this letter, since otherwise it will be considered as a newly submitted manuscript. You can access the revision submission by clicking on the link Manuscripts with Decisions in your Author Center.

Sincerely,

Julia Schroeder